THE SCIENCE AND ART OF RESTORING THE LIFE APPEARANCE OF DINOSAURS AND THEIR RELATIVES

A Rigorous How-to Guide

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That inherent uncertainties in the fossil record allow wide latitude in interpreting the life appearance of extinct animals is an unsubstantiated truism and one that hinders the practice and acceptance of paleontological restoration as a scientific discipline. It is also responsible for many inaccuracies that continue to plague dinosaur restorations.

Enough evidence is available to restore many dinosaur species with a very high degree of fidelity. This is especially true of certain duck-billed dinosaurs, whose abundant, articulated skeletons, trackways, and mummified remains allow them to be restored almost as precisely as some recently extinct animals. The skin of duckbills features dorsal midline frills and vertical shoulder folds. Among other dinosaurs, the horned dinosaurs bore unusually prominent scales and head-frill ornaments. Ankylosaurs show exceptional restorative potential because of their armor coverings. The body form of predatory dinosaurs is very like that of their avian descendants. All dinosaurs walked with a fully erect, narrow trackway gait. Most dinosaurs, even many giant forms, could run well; only sauropods, stegosaurs, and nodosaurs could not. Thecodonts, crocodilians, and pterosaurs offer important models for interpreting their dinosaur relatives, and vice versa.

Paleontological restoration is a discipline as valuable to the field as its other branches. At their best, when rendered with daring and boldness, restorations are also a form of art.

Detail of Figure 21

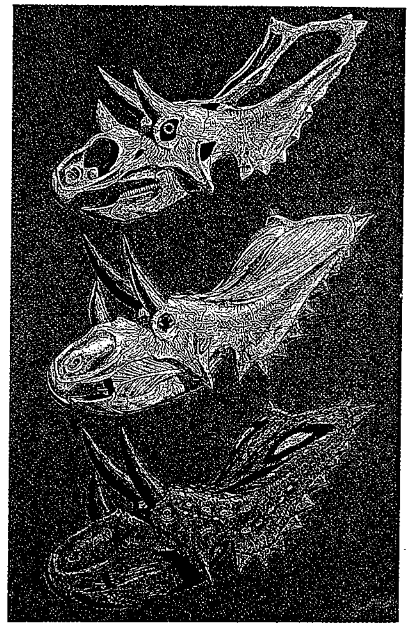


Figure 1. *Chasmosaurus "kaiseni"* skull studies showing the bare skull (top), restored muscles, keratin sheathes, and other soft tissues including pinnate cheeks, powerful frill-based jaw muscles, and hornlets and bosses (center), and restored life appearance (bottom) with skin extrapolated from skin preserved on other parts of body. Checklist 81.

The opening of the Como Bluff and Bernissart quarries in the 1870s provided artists with the first complete skeletons from which to restore dinosaurs. Since then artists have sometimes been ahead of the paleontologists. One fairly recent illustration showing a juvenile and adult *Triceratops* side by side was accompanied by a caption cautioning that such domestic scenes were as unlikely as they were appealing! Indeed, a frequent criticism of dinosaur restorations was that they made them too like birds or mammals. Although paleoillustrators have been vindicated on such points, restoring extinct animals remains an unappreciated side branch of paleontology. It is often assumed that because we cannot observe live dinosaurs we can at best restore them only approximately. This recalls the assertion of Comte (1835) that since astronomers could not directly sample stars they would never be able to know what they are made of. The result has been a damaging laissez-faire attitude about constructing dinosaurs, with skeletons still being mounted with wide-gauge trackways and dragging tails. Some paleontologists continue to approve restorations that cannot even contain the skeletons they are allegedly based upon; and museums are purchasing grossly inaccurate large-scale motion models. High-fidelity skeletal reconstructions of many basic dinosaurs, *Allosaurus, Brachiosaurus, Camarasaurus,* and *Stegosaurus* among them, have yet to be published.

In preparing a study on hadrosaur dinosaurs I was especially disturbed and chastened to find that no one, including myself, had correctly restored these most restorable of dinosaurs. Nearly complete, sometimes articulated skeletons and mummified remains allow some duck-billed species to be restored with a precision almost as high as those possible for some recently extinct animals whose life appearance is recorded by soft tissues and cave art.

THE BASICS

I am not attempting to present a definitive study on how to restore dinosaurs and their relatives but rather a brief overview to provide artists with basic information for accurately restoring archosaur anatomy and action. I have previously outlined the fundamentals of restoring prehistoric vertebrates (Paul 1984b; Paul and Chase, in press).

An original, detailed skeletal reconstruction based on the best available specimen or composite is very important for an accurate life restoration. Restorations based on previously published skeletal reconstructions or outline skeletal sketches usually prove to be seriously flawed. For this reason and because of past mistakes, I consider that most of my previously published works are no longer up to date, and the originals have been extensively revised. It is important to restore specific species and not only genera, even though there is often controversy about the identities of species and the specimens that represent them. It is always best to reconstruct the original or holotype specimen when possible. Also crucial are multiple-view reconstructions of at least one representative of each group. These reveal anatomical errors not always apparent in side view and detail the subject's three-dimensional structure. My skeletons are always posed in similar limb postures appropriate for their respective group, with the left hind limb pushing off. This facilitates both their preparation and comparison as does the drawing of each skeletal reconstruction to the same femur length (10.5 cm, except for pterosaurs). For these same reasons, humeri and femora are shown in direct lateral view instead of slightly everted as in life (compare Figs. 3c and 4f to 17).

McGowen (1979, 1982) properly cautions against drawing overly explicit conclusions about muscle form in extinct animals. However, much can still be done. Some of the more important muscles follow consistent origin-insertion patterns in most tetrapod groups, and some muscle scars can be positively identified. Muscle function also places limits on where muscles can be placed. In particular, muscles become ineffective when they are stretched much more than 1.3 times their resting length. Muscles should be profiled in black around the skeletal reconstructions as per Bakker (personal correspondence) and Scheele (1954). For studies of lizard, crocodile, bird, and mammal musculature see Fürbringer (1876), Romer (1923a, 1942, 1944), Knight (1947), L. S. Brown (1949), George and Berger (1966), and McGowen (1979, 1982).

Following the usual sources, I spent many years restoring dinosaurs as reptiles. But I sensed something was not right. Dinosaurs must have looked more like birds, rhinoceroses, and elephants than crocodiles and lizards. The growing evidence in the early 1970s that dinosaurs were more like birds and mammals was a revelation. But skin impressions show that over their avian-mammalian form was, at least in the big species, a reptilian veneer of scales, hornlets, and frills. Internally mammals are not the best models for detailed archosaur musculature because they evolved through an initial small-bodied "rough terrain and aboreal" phase. This has left their running descendants with unduly complex musculatures. Dinosaurs evolved in a much more straightforward manner from level-ground runners and retain simpler crocodile- and birdlike muscles. And dinosaurs had peculiarities of their own. Finally, to best know dinosaurs it is good to know their relatives, which are fascinating in their own right.

Heads Archosaur skulls are like those of reptiles and birds, and unlike those of mammals, in lacking facial muscles and having the skin directly appressed to the skull (Fig. 1). This feature makes them much easier to restore. Easily the most prominent skull muscle is the powerful posterior pterygoideus that wraps around and deepens the back third of the mandible. Jaw muscles bulge gently out of the skull openings behind the orbit and in thecodonts and saurischians also out of the preorbital opening and depression (Anderson 1936; Walker 1964; Norman 1985).

Dinosaur eyes were bird- or reptilelike not mammallike, so the iris is not surrounded by white. In big species the eyes were in the upper part of the orbit. Bony eye rings often show the actual size of the eye. Most dinosaurs had large eyes. Yet relative eye size decreases as animals get bigger, so I avoid the common tendency to make them overly large in big species. The eyes in juveniles and small species are proportionately much bigger, but even here restorations often exaggerate. Consider that the eye of the ostrich, the biggest among living terrestrial animals, does not appear oversize. The dinosaur's big eyes have been cited as evidence for both diurnal (Russell 1973) and nocturnal habits (Russell and Seguin 1982). Actually big eyes are compatible with either life habit; it is the (in this case unknowable) structure of the retina that determines the type of light sensitivity.

The outer ear in dinosaurs is a depression between the quadrate and depressor mandibulae muscle.

Vertebral columns Almost all dinosaur necks naturally articulate in a birdlike S curve. Thecodont and crocodilian necks are only very gently curved, and those of pterosaurs seem intermediate. Because the occipital condyle points somewhat downward the head is held at a sharp angle to the neck in birds, most dinosaurs, and pterosaurs. In thecodonts, crocodilians, diplodocids, and ceratopsians the occipital condyle and head are in a straighter line with the neck. Large zygapophyses that remain articulated over a wide range of motion indicate that archosaur necks were generally quite flexible. Powerful side neck muscles often formed a contour over the weaker ventral muscles. Since no bony elements are directly involved, the muscles under the midneck are among the most difficult to estimate. I arbitrarily make them shallow.

In many reptiles, mammals, and birds the trunk vertebrae articulate in a straight line. Thecodonts, crocodilians, pterosaurs, and dinosaurs differ in having more strongly beveled dorsals that form a dorsally convex arch. Small zygapophyses and in many cases ossified interspinal ligaments indicate that dinosaurs had stiff backs. The sacrals generally continue the line of the dorsal column.

It cannot be overemphasized that of the many thousands of dinosaur trackways, quadrupedal and bipedal, only a tiny minority show tail-drag marks (Fig. 2b–f; Lockley, this book). All dinosaurs carried their tails clear of the ground, even the whip-tailed sauropods and club-tailed ankylosaurs. Trackways indicate that many thecodonts also carried their tails clear of the ground (Fig. 2a). Pretensed upper tail ligaments probably held the tail up at little energy cost. Dinosaur tail muscles and fat may not have bulged beyond the limits of the bones so they would not overload the tail, and this is confirmed by hadrosaur tail-skin impressions

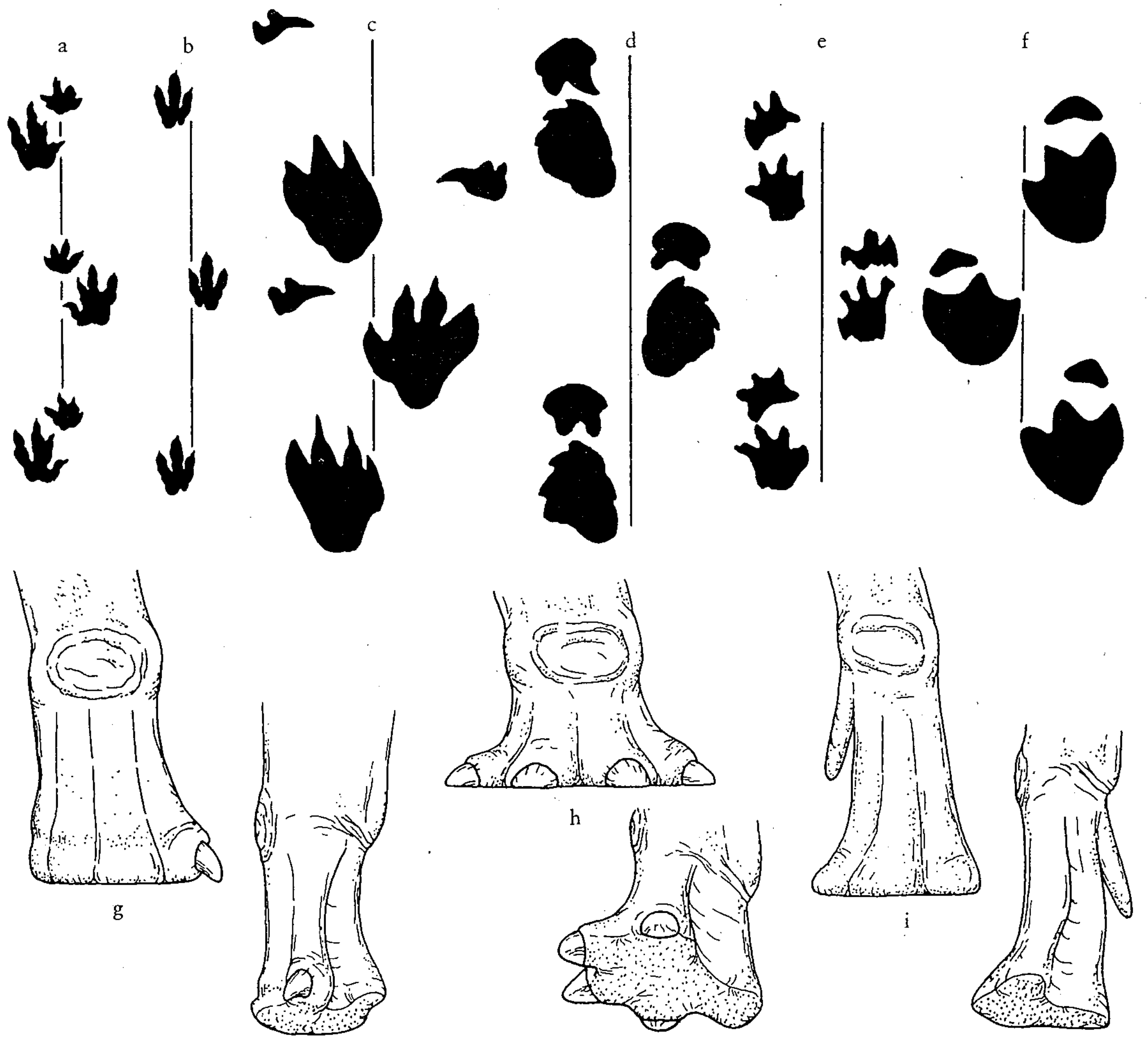


Figure 2. Top: Trackways of derived thecodont (a), large theropod (b), prosauropod (c), sauropod (d), nodosaur (e), and iguanodont (f), drawn to same stride length. Note that there are no tail drag marks and that the hands are always hollow at the base and facing partly outwards. Bottom: Restored hands of sauropod *Brachiosaurus brancai* (g), nodosaur *Sauropelta edwardsi* (h), and hadrosaur (i), not to same scale. Data from Janensch (1961), Haubold (1971), Baird (1980), Currie (1983), Carpenter (1984), and Bird (1985).

(B. Brown 1916; Horner 1984). Large zygapophyses indicate that most thecodonts and dinosaurs had fairly flexible, but not serpentine, tails.

Ribcages, bellies, and hips Like those of crocodilians and birds, the anterior ribs of dinosaurs are usually strongly swept back in articulated dinosaur skeletons of all types (Osborn 1912; B. Brown 1916, Maryanska 1977; Norman 1985: 43, 61, 90, 103, 121, 144), in thecodonts (Ewer 1965: fig. 20; Cruickshank 1972; Romer 1972), and in pterosaurs (Eaton 1910: pl. VII; Wellnhofer 1970, 1975). This is little noticed, and many dinosaur skeletons are mounted with vertical anterior ribs. Normally the chest is slab sided, and since the rib heads are offset swinging them forward overbroadens the chest and misarticulates the shoulder girdle. The belly ribs tend to be more vertical, but this condition is variable. Dinosaur trunk vertebrae and ribs form a short, fairly rigid box, with the shoulder and hip girdles close together so that the trunk musculature is rather light, like that of a bird. The longer, more flexible trunks of thecodonts indicate more powerful muscles. In all archosaurs the iliocostalis muscles continue the profile of the iliac blade onto the trunk.

All herbivores must have large digestive tracts to constantly contain the large bulk of plant material needed to sustain the healthy gut flora critical to plant digestion. Spacious posterior ribcages and hadrosaur mummies (B. Brown 1916) confirm that herbivorous dinosaurs have big bellies, so restorations that show them with hollow bellies are incorrect. In sharp contrast are big predators that gorged at a carcass, then fasted until hungry enough to hunt again. The poorly ossified, jointed abdominal ribs of predatory thecodonts and theropods are flexible, and these animals should be given hollow bellies when shown hunting.

The digestive tract and reproductive organs exit behind the ischium not under the pubis as indicated by M. Hallett (in Wexo 1985).

The dinosaur hip, especially the theropod's with its long downwardly projecting pubis and ischium, has long perplexed artists (Figs. 11, 14). Since the pubes and ischia of theropods are narrow and united along most or all of their midline, they bar the guts from between these two bones. Therefore, they were connected only by a thin tension sheet of connective tissue. To have been most effective this sheet should have stretched in a gentle concave arc between the tips of the two elements. As in living reptiles the lower tail muscles should also have run in a gentle tension curve from the tip of the ischium to the chevrons, and this is confirmed by hadrosaur mummies (B. Brown 1916; Currie personal communication). The side of the pubis had only a thin muscle running up to the upper end of the femur, and the side of the ischial rod was unmuscled. The hips of some thecodonts with long pubes are similar (Fig. 8b), and prosauropod and sauropod hips are built on the same basic plan except that they are broader (Figs. 15, 17). So the derived-thecodont saurischian lower hip was a laterally flattened tension brace unconnected to the thighs. In protobirds and ornithischians the pubis was swung backward parallel to the ischium, slinging the guts between the legs (Figs. 13, 18–20, 23, 25). In these the lower hip was a posteriorly tapering belly between the thighs. The dinosaur pubis and ischium were not submerged in flesh as often shown, but the ischium or its tip should not project out as in some restorations. Such restorations may have been inspired by the externally prominent ischia of kangaroos, but their ancestors had the usual reduced mammalian tail and are not good models for dinosaurs.

Shoulder girdles and fore limbs Dinosaur coracoids articulated with the grooved edges of a cartilagenous anterior sternum, which is in front of the paired posterior sternals (Norman 1980). The latter articulated with the first long pair of dorsal ribs via a short sternal rib. This allows the position of the shoulder girdle to be determined with confidence. Because the anterior ribs were backswept, the coracoid was under the neck-trunk juncture, not in front of it. Most distressing are reconstructions showing the coracoid jammed against the ribcage (Santa-Luca et al. 1976). In the narrow-chested thecodonts and most dinosaurs the plane of the scapulacoracoid was fairly parasagittal as in chameleons. The exceptions are protobirds and pterosaurs whose very birdlike retroverted coracoids faced anteriorly. In side view thecodont and dinosaur scapulacoracoids were usually fairly vertical, as in most tetrapods, and not horizontal. Because of their elongated, retroverted coracoids, only pterosaurs, protobirds, and birds have horizontal scapula blades.

Articulated skeletons show that scapulacoracoid orientation is variable in quadrupedal dinosaurs. This is compatible with the chameleonlike scapulacoracoid rotation suggested by Bakker (1975, this book). Dinosaurs lack a clavicle-interclavicle brace. This can be explained only as a means of freeing the coracoid to glide fore and aft in the sternal groove. Likewise chameleons, turtles, crocodilians, and mammals have freed the shoulder girdle by unbracing it (Peterson 1984; Nicholls and Russell 1985). Nicholls and Russell, however, are incorrect in attributing scapular mobility to all birdlike theropods; in many the large fused furculae and big sternal plates immobilized the shoulder girdle (Fig. 14; Barsbold 1983; Paul and Carpenter, in preparation). Note that the vertically oriented scapulacoracoid does not cut off the throat or perform other anatomical violations as it swings forward, contrary to Bennett and Dalzell (1973). Scapular rotation is important because the shoulder joints swing fore and aft relative to one another during the limb cycle, a mammallike attribute.

Contention still surrounds the issue of dinosaur fore-limb posture. This is unfortunate since trackways of all species show the narrow fore-print gauge typical of a fully erect gait (Fig. 2c–f; Bakker 1971a; Lockley, this book). Crucial to the issue is the relative orientation of the shoulder joint. Especially informative in this regard are chameleon shoulder girdles, which are so amazingly like those of dinosaurs that one found in Mesozoic sediments would be identified as a tiny dinosaur (Fig. 3b). The chameleon shoulder glenoid is much more inwardly directed than in crocodilians and lizards, partly because the scapulacoracoid is flatter relative to the body wall. As a consequence chameleons have a much more vertical humerus action (Peterson 1984; Bannister 1984). With the scapulacoracoid also in a nearly parasagittal plane the scapular portion of the dinosaur shoulder glenoid actually faces slightly inward (Fig. 3c–d). This can only mean a nearly vertical humerus action, with the elbow tucked in close to the body. This is confirmed by the orientation of dinosaur hand prints, which, as Carpenter (1982) explains, invariably face outward (see Fig. 2c–f). Facing both the hand and elbow outward requires that the radius and ulna be uncrossed, but this is not possible in dinosaurs because they have moderately crossed, partly or completely interlocking radii and ulnae (Fig. 3c–d, note that the radius articulates with the outer humerus condyle and the inner wrist bones; a number of recent skeletal mounts do not reflect this basic fact). In fact a sprawling gait requires freely rotating lower arm elements that will not twist the foot on the ground as the arm pivots backward. Detailed articulations show that dinosaur elbows are only moderately bowed out some fifteen or more degrees, excepting rectigrades in which it is less (large deltoid crests obscure this elbow eversion in the skeletal front views, and these show the minimum elbow eversions of high speeds). The beveled end of the radius bows the wrist inward a little. Ungulates have similar limbs (see front views in Nowak and Paradiso 1983; Norman 1985: 139).

Trackways prove that the advanced rauisuchid thecodonts also had narrow trackways and outwardly facing hands (Fig. 2a). With more outwardly facing shoulder joints and flexible radii and ulnae their elbow was more bowed out (Fig. 8). More primitive thecodonts, such as *Euparkeria,* and eurythrosuchids and phytosaurs had wider, semierect fore limbs; the ancestral chasmosaurs were full sprawlers (Bakker 1971a; see Lockley, this book, on phytosaur fore-limb tracks). Comparative manipulation of bird and pterosaur fore limbs shows that the latter could be used for ground locomotion (contra Padian 1983). The out- and upward facing shoulder joint means a sprawling fore limb, with the elbow flexed down ninety degrees from the horizontal humerus to give the hands a narrow trackway. That even the marine *Pteranodon* retains fully functional fingers confirms that it moved with its hands.

Having dealt with transverse fore-limb posture, we turn to fore and aft posture. Most dinosaurs are "primitive" in having backwardly directed shoulder glenoids and humerus heads that wrap far onto the back of the humerus (Bakker 1974). This flexes the shoulder and elbow, so that the humerus slopes down and backward as in ungulates (Fig. 3c). Because of the shoulder girdle's mobility and the open shoulder joint the humerus could protract to vertical (contra Bennett and Dalzell 1973).

In nodosaurs, sauropods, and stegosaurs the shoulder glenoid faces much more downward, and the humerus head does not wrap as far backward. Also, the distal humeral condyles do not wrap as far forward as in other dinosaurs. These are derived characters, and they show that the humerus was vertical and the elbow was straight in these elephant-limbed or rectigrade dinosaurs (Fig. 3d; Bakker 1971a).

All dinosaur and pterosaur hands were either digitigrade or unguligrade, and the wrist was stiffly held straight or close to it during the propulsive stroke. None had the flat, plantigrade hands retained in thecodonts and crocodilians. All archosaurs could hyperflex the wrist; even elephants flick the wrist back ninety degrees to clear the hand during recovery. It is important to remember that no archosaur had hands that looked like the feet. Due partly to different bone structures their fore feet always lack a heavy central pad and are hollow behind, giving them a distinctive half-moon shape (Fig. 2c–i). In hadrosaurs, iguanodonts, sauropods, and stegosaurs the fingers are united into a pseudohoof in that they are encased in a single lunate pad, with most or all of the single hooves lost. A very distinctive character of theropods, prosauropods, and some sauropods and ornithischians (including iguanodonts) is the big clawed, inwardly-divergent-when-extended thumb weapon. It was often held clear of the ground when walking. Birds retain this medially divergent thumb as the feathered alula, or wing slot. Thecodonts, crocodilians, and pterosaurs lack inwardly pointing thumbs.

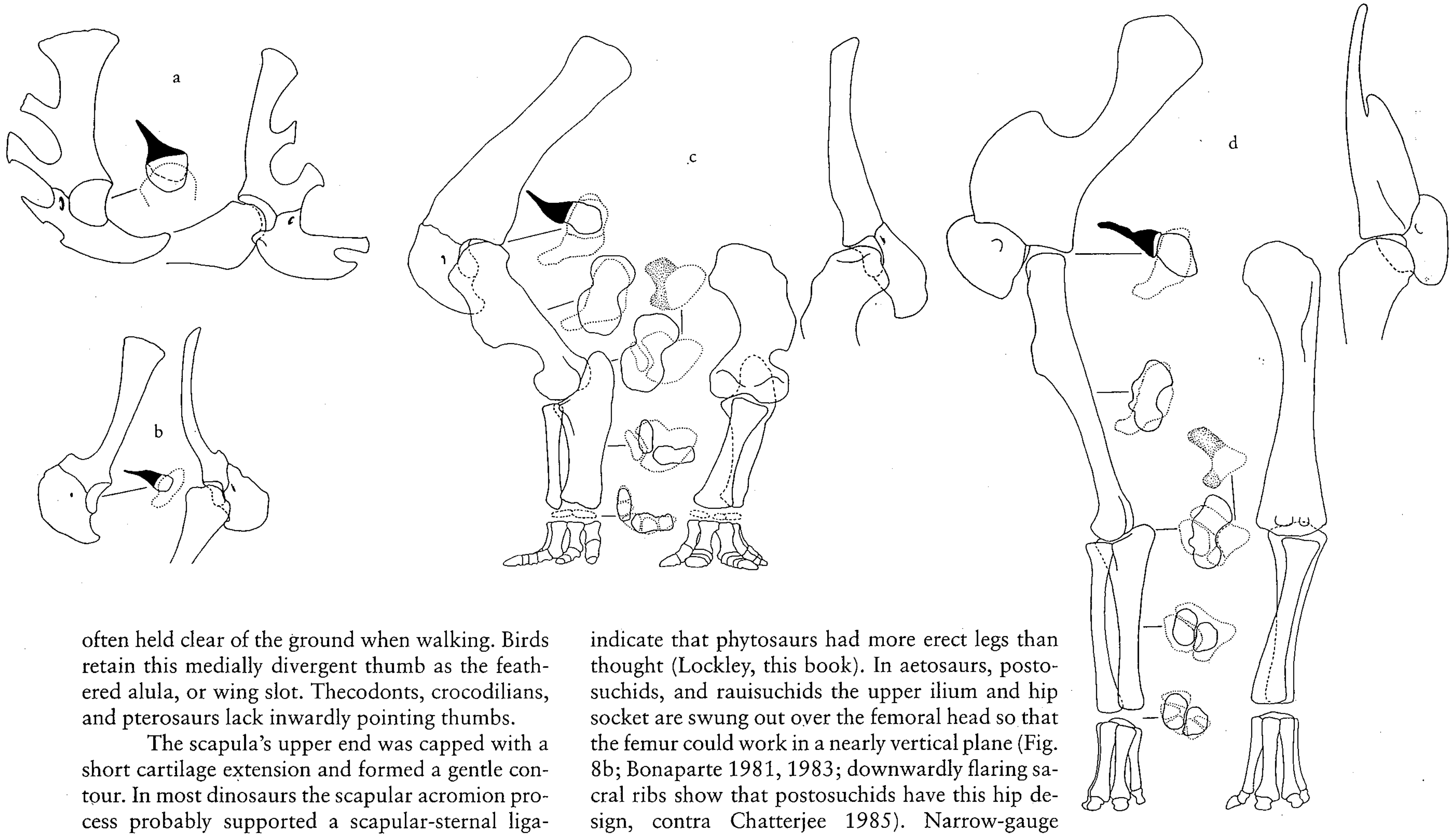


Figure 3. A comparison of left shoulder joint orientation, fore-limb posture, and joint articulation in the lizards *Iguana* (a) and *Chamaeleo* (b), the flexed-limbed dinosaur *Triceratops horridus*, USNM 4842 and AMNH 970 (c), and the rectigrade *Brachiosaurus brancai*, HMN SII and HMN Sa9 (d, compare to Fig. 17). Stippling indicates the ulnar articular facets for the humeral condyles as distinct from the olecranon process. Not to scale.

The scapula's upper end was capped with a short cartilage extension and formed a gentle contour. In most dinosaurs the scapular acromion process probably supported a scapular-sternal ligament, which in turn supported the clavicular deltoids. The proximal end of the humerus bulged out a little, and in many but not all dinosaurs a very large deltoid crest formed a prominent contour along the entire length. The triceps was a prominent contour muscle. The scar for the latissimus dorsi is unusually far down, opposite the deltoid crest's lower end where it formed a prominent contour above the arm pit. Hand flexors and extensors bunched around the elbow and operated the hand via tendons; the wrist formed a bulge.

Hind limbs Hip morphology suggests that chasmosaur hind limbs were sprawling, and that euparkerids, eurythrosuchids, and phytosaurs were semierect (Fig. 8a; Bakker 1971a). But trackways indicate that phytosaurs had more erect legs than thought (Lockley, this book). In aetosaurs, postosuchids, and rauisuchids the upper ilium and hip socket are swung out over the femoral head so that the femur could work in a nearly vertical plane (Fig. 8b; Bonaparte 1981, 1983; downwardly flaring sacral ribs show that postosuchids have this hip design, contra Chatterjee 1985). Narrow-gauge trackways confirm their erect gait. The protodinosaur ornithosuchids, protocrocodilians, and early pterosaurs have rather dinosaurlike hip joints that indicate a fairly erect hind limb. Advanced pterosaurs, however, have secondarily reverted to semierect legs.

The crocodilianlike thecodont knee appears to be flexed, but as in crocodilians the hind limbs are so flexible that the femur can retract well past vertical and the knee can straighten.

Heerden (1979) and Martin (1984) suggest that prosauropods and protobirds walked with a wide, semierect gait. But, like those of all dinosaurs, trackways show that prosauropod hind limbs followed a narrow-gauge trackway (Baird 1980; Olsen and Galton 1984). The characters

Heerden cited as evidence of a semierect gait are actually the same as those found in the fully erect birds, *Archaeopteryx,* and most other dinosaurs. These all share similar limbs in which the knee is bowed out moderately, especially as it swings forward and clears the gut (the skeletal back views show the minimal, high-speed knee eversion), and the ankle is bowed inward slightly (see the ostrich in Muybridge [1887] 1957; pigeon in Cracraft 1971; Santa-Luca 1980). Ungulates are also similar (see rear views in Muybridge [1887] 1957). In the rectigrade sauropods and stegosaurs the knee was less bowed out. Knight (in Massey-Czerkas and Glut 1982: 35, 80), Parker (in Swinton 1970), and Spinar and Burian (1972) occasionally splayed out dinosaur hind limbs too much.

In side view, inadequately considered hind-limb action afflicts many restorations. Newman (1970), Galton (1970), Hotton (1980), Cooper (1980), and Hallett (in Wexo 1985) give varying accounts of how bone strengthening around the hip socket affects posture and limb action. The greatest normal stress in animals is up- and forward as the hind limb pushes the body in the same direction. Severe abnormal stresses include a back- and upward shock if a foot missteps. Hence, dinosaur hip joints are well strengthened both fore (sometimes by sacral ribs, Maryanska and Osmolska 1984), and aft, as well as above. Hip-joint stressing tells us therefore little about posture.

What tells us more is the expanded posterior portion of the acetabulum, or antitrochanter. Also found in birds, it remains fully articulated with the femoral head as the femur swings from about sixty degrees forward of vertical to about vertical (except for sauropods and stegosaurs). Contrary to usual opinion, photographs and films show that femoral action is this extensive in fast-running birds (see Fig. 5; Ricciuti 1979; Boswell and Mansfield 1981; Chadwick 1983). Either rearing the body up too high or hyperretracting the femur partly disarticulates the hip joint. It also overshortens the ischial-based femoral retractors. Rearing, therefore, is tolerable only at slow speeds.

Charig (1972) argues that normally walking saurischian-hipped dinosaurs tilted up to avoid a supposed "knee-knocking-on-the-pubis" problem. However, much of the pubioischiofemoralis internus functions to keep the femur erect in these dinosaurs rather than to protract it, and plenty of other muscles are available to protract the femur forward of the pubis.

Dinosaur and pterosaur knees are very birdlike. A large "roller" inner femoral condyle bears most of the load. Meanwhile a thin angular outer condyle runs in a groove between the tibia and fibula and prevents the knee from twisting about its long axis (Fig. 4a–c). In most post-thecodont archosaurs the knee cannot be straightened because to do so would rotate the outer condyle out of its groove and leave the knee open to complete dislocation. This is true even of such giants as *Tyrannosaurus rex, Triceratops,* and *Shantungosaurus.* The orientation of the hip and knee joints shows that most dinosaurs had bird- or ungulatelike femoral posture and action in which the knee always stayed flexed (Fig. 4a–c, e) and the femur never retracted past vertical (Tarsitano's 1983 restoration of dinosaur hind-limb action is especially out of line with this evidence). Indeed overall limb action must have been very like that of fast birds and mammals with the femur providing the main propulsive stroke (Fig. 5).

In sauropods and stegosaurs the antitrochanter is reduced or absent; and so the femur can retract past vertical. In addition, the fibula-calcaneum unit is longer than the tibia-astragalus so that the fibula head can rise above the tibia head (Fig. 4d) and brace the outer femoral condyle even when the knee is straight. The femur is therefore vertical in these rectigrades (Fig. 4f).

Most dinosaurs and pterosaurs had simple, birdlike hinge-jointed ankles that hyperflexed to clear the foot from the ground during recovery. The sauropod's and stegosaur's very short, broad metatarsi and toes, backed by a very large pad, indicate, however, a fixed ankle. Dinosaur metatarsi were always tightly interbound; the frequency with which articulated pterosaur metatarsals are splayed apart suggests increased suppleness. Like the hand, all dinosaur and pterosaur feet are digitigrade or unguligrade, never plantigrade; nor were they ever semiunguligrade like ostriches—certain trackways that suggest so are reflecting the distribution of pressure along the toes (Thulborn and Wade 1984). Most dinosaurs probably let their toes droop during recovery as do the big ground birds (toe clenching is limited to perching birds). Sauropod and stegosaur toes were relatively immobile. The four-toed basal predatory dinosaurs, prosauropods, segnosaurs, and some ornithopods bear large hind claws. They and the big-clawed early theropods may have balanced on their robust tails and kicked out like dinosaurian kangaroos (Marx 1978: fig. 1; Bakker personal communication). Thecodont metatarsi and feet were always supple and plantigrade, and the complex ankles are rather mammallike with a long calcaneal tuber in the heel. Suggestions by Walker (1964), Sill (1974), and Chatterjee (1985) that advanced thecodonts were digitigrade are not supported by the typically thecodontian ankles and feet found in these animals. In dinosaurs toe 5 is reduced to a splint or lost.

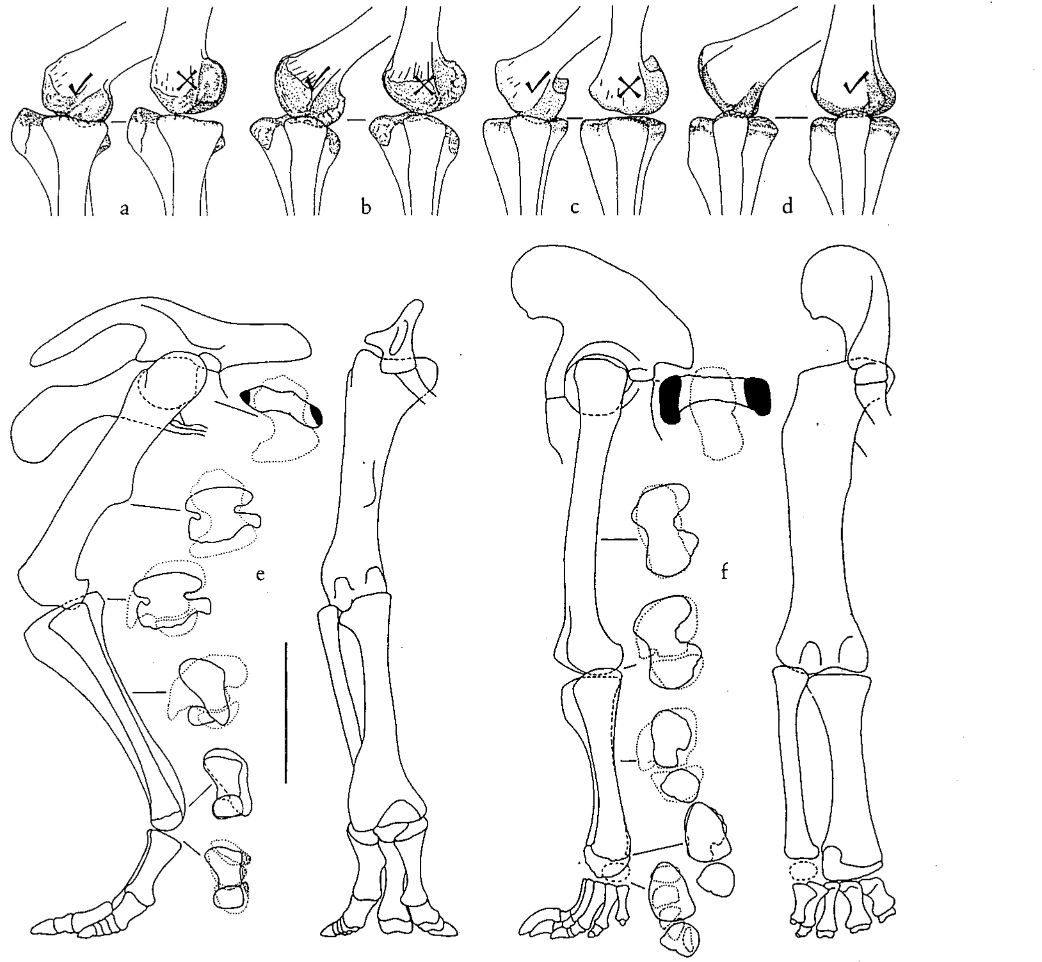


Figure 4. Top: The articulation of the left knee in the giant flexed-jointed *Tyrannosaurus rex*, CM 9380 (a), *Triceratops horridus*, USNM 4842 (b), and *Shantungosaurus giganteus*, PMNH 5 (c), and in the rectigrade *Stegosaurus ungulatus* YPM 1858 (d). On the left the knees are flexed with the outer femoral condyle running in the groove made by the fibula and tibia. On the right the knee is straightened, which works only in *Stegosaurus* in which the fibula is proximally extended and continues to brace the outer femoral condyle. Bottom: A comparison of hind-limb posture and joint articulation in the flexed-limbed dinosaur *Kritosaurus incurvimanus*, ROM 764 (e) and the rectigrade *Brachiosaurus brancai*, HMN specimens (f, compare to Fig. 17). Stippling indicates hypotarsi; data in part from Janensch (1961), Ostrom and McIntosh (1966, especially pl. 49) and Hu (1973). Not to scale.

The tail-based caudofemoralis femoral retractor muscle forms a prominent contour (its profile is seen under the more superficial muscles in muscle restorations), excepting, of course, in the tailless pterydactyloids and birds. The evolution of the archosaur ischium and the femoral retractors it supports is very interesting. In basal thecodonts and pterosaurs the ischium is a short, broad lizardlike apron that anchored a number of femoral retractors. The ischial rod found in advanced thecodonts and most dinosaurs is too slender to have anchored femoral retractors; in addition, such distally placed muscles would have been badly overstretched during normal limb action. Instead, the rod is a tension brace. In protobirds and birds, who have returned to the thecodont condition, the rod is lost as the tail is reduced.

Lizards and crocodilians are good models for restoring thecodont hind limb and foot muscles,

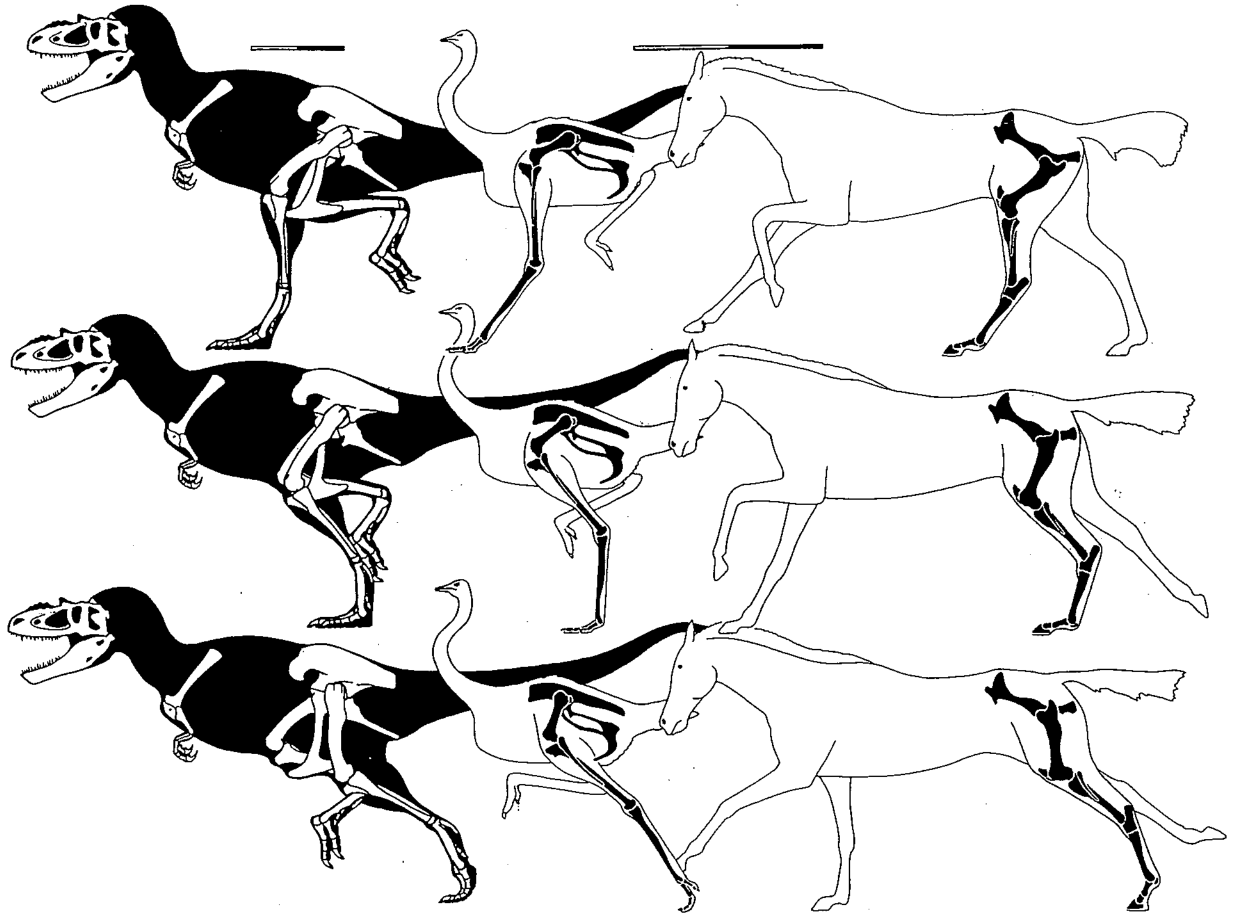


Figure 5. Comparison of hind-limb action in fast-running thoroughbred, ostrich, and *Albertosaurus libratus.* Bone positions are approximate; note the similarity of the animals' hind-limb action including extensive femoral action. Scale bars equal 1 meter. Data for ostrich from Chadwick (1983) and Boswell and Mansfield (1981); data for horse from pl. 71 in Muybridge ([1887] 1957).

and the achilles tendon is very prominent above the calcaneum tuber. Pterosaurs and dinosaurs differ greatly in having much more bird- or ungulatelike hind-limb muscles. In particular, the thigh is laterally flattened but antero-posteriorly broad, a fact recognized by Romer (1923b, 1927). One of Knight's greatest and most persistent errors was to show dinosaurs with narrow, reptilelike thighs (in Massey-Czerkas and Glut 1982). The anterior expansion of the iliac blade supported an enlarged, birdlike anterior iliotibialis in sauropods, segnosaurs, and theropods, and not just ornithischians. In pterosaurs and most dinosaurs the knee's large cnemial crest and the birdlike feet show that a powerful "drumstick" of extensor and flexor muscles operated the feet via long tendons (Bakker in Russell 1973; Glut 1982; Padian 1983). The gastrocnemius and achilles tendon were prominent as they ran behind the leg and ankle to the foot. As in birds the ankle joint must have been very prominent, with grooves running between the upper and lower tarsals.

Exceptions to the normal pattern are again the sauropods and stegosaurs. There is a tendency to restore their limbs as heavily muscled pillars, but since the foot is immobile the shank muscles that operate it are weak. Indeed the shin was hardly muscled at all, as in humans and elephants (see Knight 1947). The ankle joint was buried in the great foot pad.

Speed A pack of running tyrannosaurs attacking a herd of charging ceratopsians makes for a dynamic restoration (Fig. 6). The image, however, is difficult to accept because we are accustomed to a modern world that is biased against big runners; there are no giant predators, so there is little incentive for big animals to be fast. Indeed, it is widely, but not universally, accepted that stress loads and design constraints prevent very large animals from running.

Actually the ability to run is normal among terrestrial animals. A run is when all the limbs leave the ground simultaneously in a ballistic suspended phase, including hopping, the bipedal run, the trot, pace, and various gallops. Among living medium-sized and big animals only elephants and tortoises cannot run. In fact, most animals run very well, better than we humans. As for size, no stress, scaling, or morphological analysis establishing that big size does bar high speeds has been published. Scaling, mechanical, and energetic studies do indicate that big animals enjoy important advantages over small animals and can be fast (Heglund et al. 1982; McMahon 1984; Lindstedt et al. 1985). Indeed, a 3.5-metric-ton white rhino can gallop (Guggisberg 1966), and 1.8-metric-ton black rhinos are reported to outsprint horses (Muybridge [1887] 1957). The real question is not whether dinosaurs could run, but whether any could not.

Elephants and tortoises cannot run because they have very strange limbs, with fixed ankles that cannot rotate more than a few degrees. The effects of this can be simulated by trying to run on your heels alone. Medium-sized and larger animals with flexible ankles that can push the body into a long, suspended phase can run; there are no exceptions.

Among dinosaurs only sauropods and stegosaurs have a fixed ankle; the limbs of other dinosaurs are of the peculiar columnar elephantine type (rectigrade) compatible with a slow, ambling gait (Fig. 7; Muybridge [1887] 1957; Bakker 1971a, b, c). Coombs (1975) suggested that sauropods were slower than elephants because they lack elbow and ankle leverage, criticism sometimes leveled at dinosaurs in general. It is contradicted by the fact that quadrupedal dinosaurs have large olecranon processes and hypotarsi.

All other dinosaurs have fairly long birdlike ankles and feet and so could run. Many trackways show small to very large dinosaurs running (Farlow 1981; Lockley et al. 1983; Thulborn and Wade 1984; Matsukawa and Obata 1985). As with humans, however, a flexible ankle does not guarantee high speeds of more than fifty kilometers per hour.

A basic fast running limb design includes long bird- or ungulatelike limbs with powerful, proximally concentrated muscles, deep shoulder and hip sockets, cylindrical flexed spring-action joints, tibiae and metatarsi that together make up at least ninety percent of the femur's length, large olecranons and hypotarsi, and laterally compressed, functionally three-toed, lightly padded, digitigrade or unguligrade feet. All living animals with such limbs run well. Excepting sauropods, stegosaurs, and to a certain degree nodosaurs, all dinosaurs—including the biggest ornithopods, ceratopsids, and tyrannosaurs—also have all of these limb adaptations (Bakker 1971a, Paul, in press, a). Tyrannosaurs are especially important because they share the same limb anatomy as the ostrich-mimic theropods (McMahon 1984: figs. 4–9). Far from being dinosaurian tortoises and elephants, most dinosaurs were involved in a predator-prey size and speed race. It is not surprising therefore that one trackway appears to show a small bipedal dinosaur running some seventy kilometers per hour (suggestions by Welles [1971] and Thulborn and Wade [1984] that a hyperlong limbed walking dinosaur made this track are unsupported by any evidence). Especially unacceptable are suggestions that even small, gracile dinosaurs were built only for walking and speeds of thirteen kilometers per hour (Halstead and Halstead 1981; Hotton 1980).

Integument and claws Skin impressions are known from a number of large dinosaurs. They show that dinosaur scales were always nonbony, mosaic patterned, and never overlapping. Even in big species the skin appears to have been thin. One hadrosaur mummy indicates that the thigh skin made a smooth unfolded transition onto the trunk, and this may have been true of other dinosaurs as well. Prominent frills and skin folds are sometimes preserved; these, dewlaps, wattles, and other soft display organs may have been more common than we realize.

Some suggest that since big dinosaurs are known to have naked skin, small dinosaurs and thecodonts should have the same. Especially fascinating in this regard are the preserved insulation coats of some small archosaurs. These include the long body contour scales in longisquamid thecodonts (Sharov 1970; not to be confused with the elongated "dorsal scales"), pterosaur fur (Sharov

1971), and *Archaeopteryx*'s famous feathers. I do not know of a single case of mosaic scales in small dinosaurs or thecodonts. (It is enlightening to consider that if future nonhumanoid paleontologists living in a nonmammalian world find only human, rhino and elephant skin impressions, they might conclude that all mammals were naked skinned!) There is skin preserved in small *Thescelosaurus,* but Gilmore (1915) noted that it had a "punctured" instead of a scaled surface (this impression is not currently accessible). The difference of this small ornithopod's skin from the big ornithopod's indicates that it served a different purpose. The punctured surface may have supported an insulative covering. If small archosaurs were so insulated, their avian relationships strongly suggest that they were feathered. Thulborn (1985) speculates that dinosaur feathers may have been contoured rather than degenerate and furlike as suggested by Feduccia (1980). Either is possible. It is also possible that the juveniles of large species were insulated, perhaps in down, which they shed as they matured.

Articulated armor tells us much about the outer appearance of some thecodonts, crocodilians, and dinosaurs. Armor plates, hornlets, bosses, and skull rugosities are almost always enlarged by horn (keratin). The bony cores of claws and hooves are likewise enlarged by horn coverings, and these are often but not always worn down at the edges or tip.

Color This aspect of restoration is most asked about, least knowable, and least important. I often do not decide the dinosaur's color until I have completed the background and see what looks best. A light tone might appear advantageous for large animals in hot habitats, but tropical naked-skinned animals such as elephants, rhinos, humans, monitors, and crocodilians are dark, as an ultraviolet radiation screen. Russell (1977) suggests that color-sighted dinosaurs should have borne color camouflage patterns. This may be correct, but earth-tinged mammals blend well into backgrounds before color-sensitive human eyes. Also significant is that big reptiles and birds tend to be earth tinged despite their color vision. The big archosaur's scales (as opposed to the bare skin of big mammals) could carry bold patterns, like those of giraffes and zebras. Small archosaurs are the best candidates for bright motifs. Archosaurs of all sizes may have used specific color displays for intraspecific communication or for startling predators. Crests, frills, skin folds, and taller neural spines would be natural bases for vivid, even iridescent, display colors, especially in the breeding season. But remember, except for the improbability of gaudy colors on the big species, any color pattern is both speculative and possible.

THE ARCHOSAUR GROUPS

Thecodonts Most thecodonts are rather long, low, crocodile-shaped animals, except that their skulls

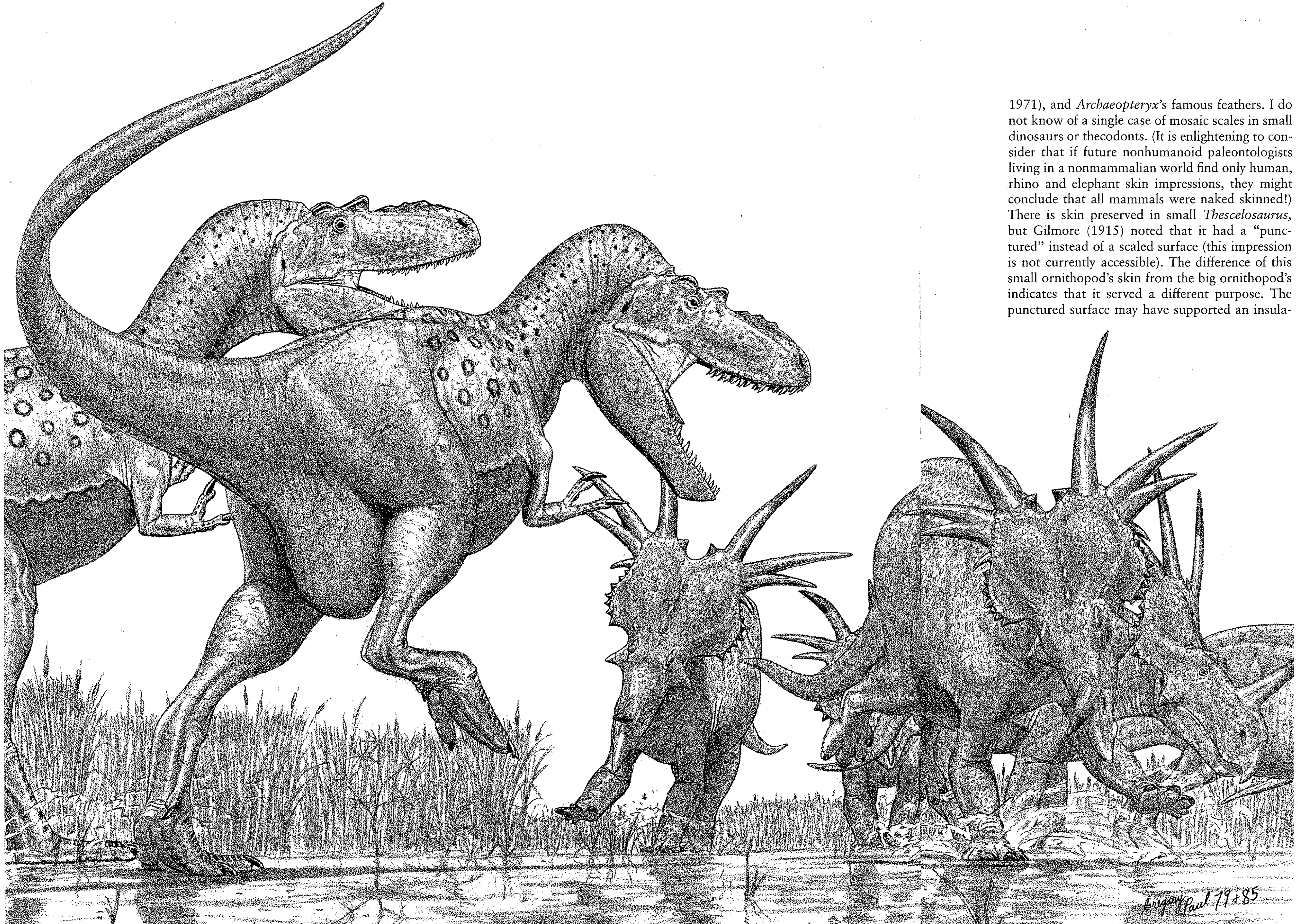


Figure 6. "An *Albertosaurus libratus* Pair Invites a *Monoclonius* (= *Styracosaurus*) *albertensis* Herd to Dinner, The Latter Firmly Decline." Like most big dinosaurs, the bird-limbed tyrannosaurs and rhino-like ceratopsids were built for speed; their combat is unrivaled in the modern world. The locale is a cattail marsh in the Judith River Formation. Checklist 68.

are deep and narrow, like those of dinosaurs (Fig. 8). Their trackways, big heads and necks, and fairly strong fore limbs show that they were usually quadrupedal, except for the short fore-limbed *Postosuchus* (Chatterjee 1985). Long, well-muscled, vertically flexible (not laterally as in lizards) dorsal columns suggest that their fastest gait was a bounding, crocodilelike gallop, even in the giant forms (Fig. 8b; Zug 1974). The supple-limbed, flat-footed, galloping, predatory thecodonts were archosaurian "bear/crocs," quite different from the birdlike predatory dinosaurs.

Many thecodonts are restored with transversely rounded skull roofs, whereas articulated skulls are usually flat as in other archosaurs. At least some thecodonts such as *Saurosuchus* (Fig. 8b) had horn decorations on their skull. Phytosaurs have highly sculpted skulls very like the crocodilians they so closely mimic.

The hands and feet have five free digits, except for a few species that lack the outer toe. The outer finger and toe were usually divergent grasping digits, as in many lizards. Claws are usually rather small, the hind feet pointed straight ahead or outward.

Most thecodonts have a row of paired scutes running along their backbone and sometimes underneath their tails. The well-known aetosaurs differ from most thecodonts in being big-bellied, small-skulled, heavily armored herbivores. Phytosaurs too bear a heavy, in their case crocodilelike, armor and are also known from many excellent skeletons. They and aetosaurs are among the most restorable of archosaurs.

The reconstruction of the *Gracilosuchus stipanicicorum* skull by Brinkman (1981) is at odds with the complete and little-crushed skull of the Museum of Comparative Zoology (MCZ 4117) with its aetosaurlike posterior skull (Romer 1972; Lewis personal communication). The skeletal reconstruction of Chatterjee (1985) of *Postosuchus kirkpatricki* is too short in the vertebral column by fifty percent. Note that ornithosuchids, which were protodinosaurs, were always small, never big as suggested by Walker (1964).

Pterosaurs I agree with Padian (1983) that pterosaur wing membranes did not connect with the hind limbs and that the hind limbs folded together for streamlining in normal flight (Fig. 9). There is evidence that the tailless pterodactyloids had an auxiliary membrane behind the hind limb (Broili 1938; Wellnhofer 1970; Paul in Parrish 1986: 79). Pterodactyloids have supple humanlike ball-and-socket hip joints and may have used the hind-limb membrane for special maneuvers, especially landings. Impressions also indicate the presence of webbed hind feet (Broili 1938; Wellnhofer 1970, 1975). These may have been used as air brakes. Instead of projecting out, the free fingers were probably appressed to the wing finger during flight for streamlining. Padian (1983) shows that most pterosaurs were powered flappers. Indeed, even the giant pterosaurs retain the smaller pterosaur's flapping adaptations, including large deltoid crests. The enormous deltoid crest, elbow joint, and carpal block of *Quetzalcoatlus* are especially contrary to

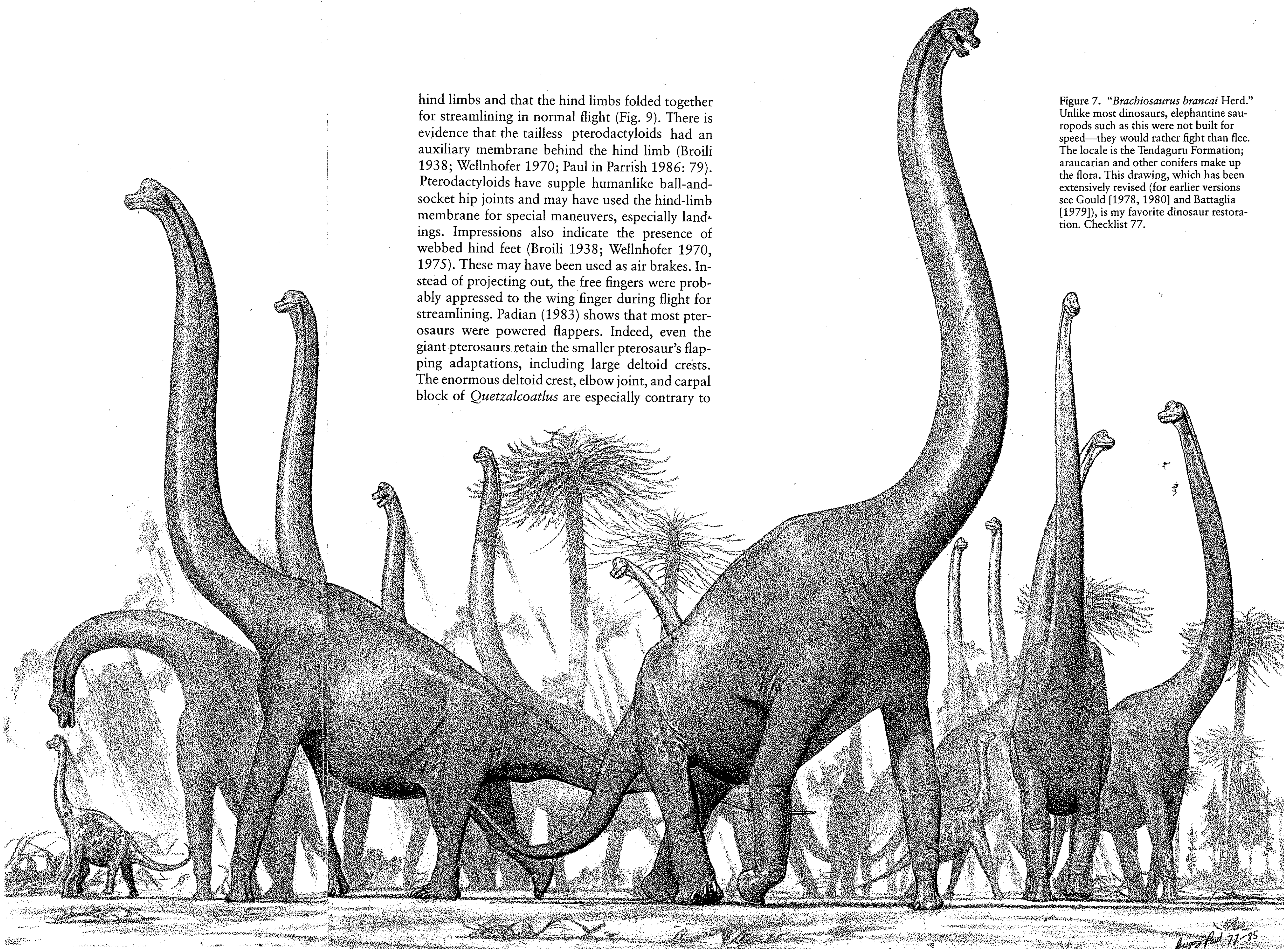


Figure 7. "*Brachiosaurus brancai* Herd." Unlike most dinosaurs, elephantine sauropods such as this were not built for speed—they would rather fight than flee. The locale is the Tendaguru Formation; araucarian and other conifers make up the flora. This drawing, which has been extensively revised (for earlier versions see Gould [1978, 1980] and Battaglia [1979]), is my favorite dinosaur restoration. Checklist 77.

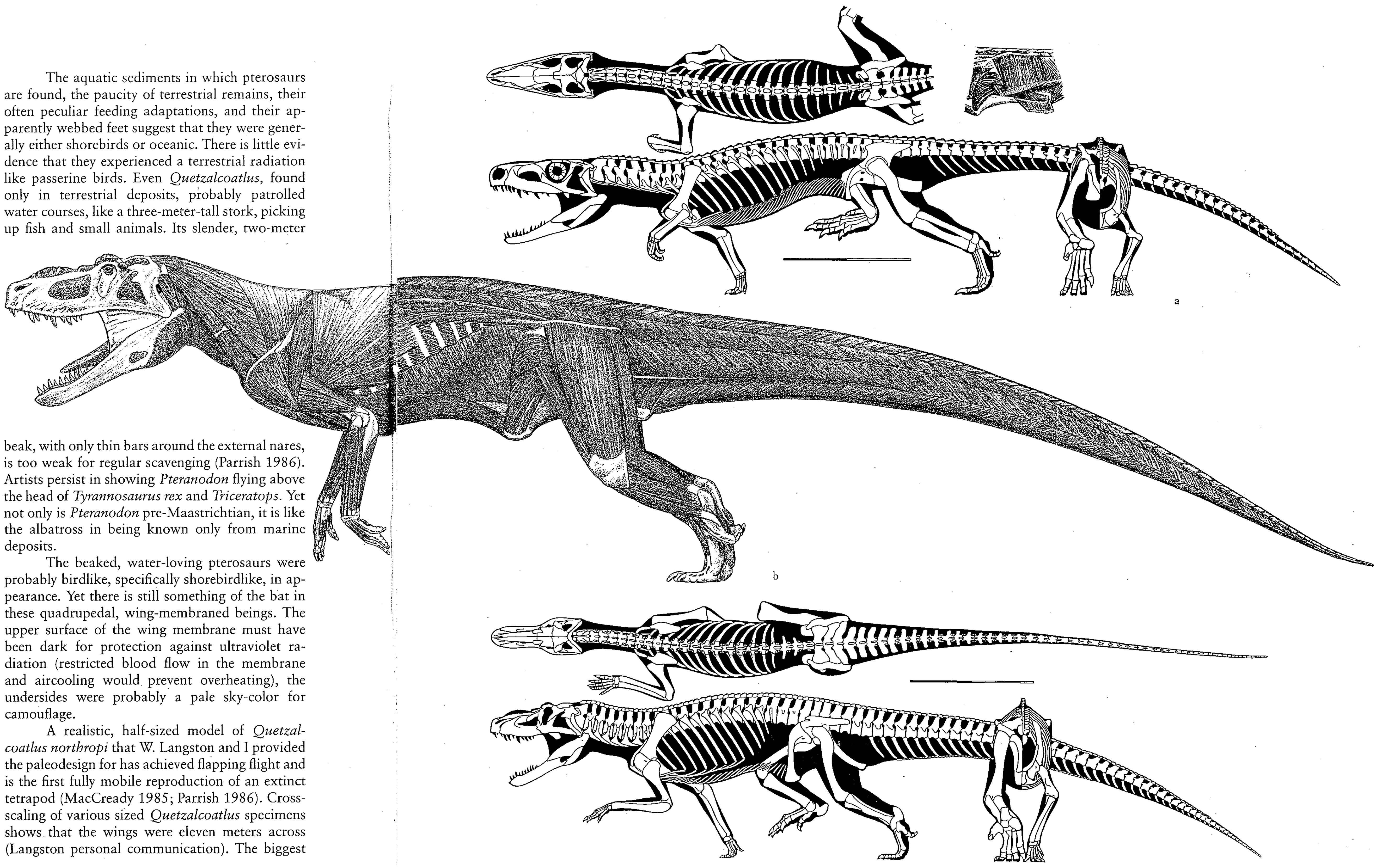


Figure 8. Two basic thecodonts. a. *Euparkeria capensis* holotype, SAM 5867. The tail is unknown, and the skull is lower than restored by Ewer (1965). Scale bar equals 100 millimeters; insert shows the hip musculature. b. A composite rauisuchid *Saurosuchus galilei* based on a complete SJM skull, many details from other rauisuchids, and data from Sill (1974) and Bonaparte (1981, 1983); muscle restoration is in a bounding gallop. Scale bar equals 1 meter, front views are reversed, proportions are approximate, and armor is not included in top views. Note downward facing hipjoint.

the streamlining expected in soarers and suggest that even the biggest pterosaurs were predominantly flappers.

Unlike broad-winged, slow-flying bats, in which the fore limb does not blend into the wing membrane, the narrow-winged, fast-flying molossid bats use fur and muscles to streamline the wing bones into the membrane (Vaughan and Bateman 1980). The narrow-winged pterosaurs were fast flyers and probably did the same (Fig. 9). Connective tissue probably continued the fore wing a short distance outside of the wrist. AeroVironment's work on *Quetzalcoatlus* aerodynamics (MacCready 1985; Parrish 1986) suggests that pterosaurs had wings like frigate birds or gulls, with a sharp reflex at the base of the wing finger and a membrane that was broadest behind this reflex. This makes them exceptionally graceful creatures.

Most pterosaurs, even those with teeth, had horn beaks lengthening their jaws. Pterosaur necks have too few vertebrae for the skull to be pulled back over the trunk as in some birds. The sharp angle between the head and neck suggests a gently upcurved neck.

Padian (1983) argues that all pterosaur hips were united along the ventral midline. Many were, but three-dimensionally preserved specimens show that *Rhamphorhynchus* has splayed out, birdlike lower hip elements (specimens in the Mineralogisk Museum, Copenhagen [MMK 1891.738 in Wellnhofer 1975] and Raymond Alf Museum, Los Angeles). Padian (1983) shows that pterosaur hind limbs are powerful running organs. On the other hand, big-headed yet tailless pterodactyloids are not well adapted for bipedality because they lack the anterior migration of the hip joint and the posterior migration of the belly that helps birds balance over their hind limbs. Their fastest gait was probably a fast quadrupedal trot. The long-tailed rhamphorhynchoids may have been more bipedal, especially *Dimorphodon* in which the elbow to finger base distance is too short for the fore limb to have been used on the ground.

The three short fingers bear large recurved claws. The four normal toes have small claws, in rhamphorhynchoids the very long, unclawed fifth toe may have helped support a web.

The aquatic sediments in which pterosaurs are found, the paucity of terrestrial remains, their often peculiar feeding adaptations, and their apparently webbed feet suggest that they were generally either shorebirds or oceanic. There is little evidence that they experienced a terrestrial radiation like passerine birds. Even *Quetzalcoatlus,* found only in terrestrial deposits, probably patrolled water courses, like a three-meter-tall stork, picking up fish and small animals. Its slender, two-meter beak, with only thin bars around the external nares, is too weak for regular scavenging (Parrish 1986). Artists persist in showing *Pteranodon* flying above the head of *Tyrannosaurus rex* and *Triceratops.* Yet not only is *Pteranodon* pre-Maastrichtian, it is like the albatross in being known only from marine deposits.

The beaked, water-loving pterosaurs were probably birdlike, specifically shorebirdlike, in appearance. Yet there is still something of the bat in these quadrupedal, wing-membraned beings. The upper surface of the wing membrane must have been dark for protection against ultraviolet radiation (restricted blood flow in the membrane and aircooling would prevent overheating), the undersides were probably a pale sky-color for camouflage.

A realistic, half-sized model of *Quetzalcoatlus northropi* that W. Langston and I provided the paleodesign for has achieved flapping flight and is the first fully mobile reproduction of an extinct tetrapod (MacCready 1985; Parrish 1986). Cross-scaling of various sized *Quetzalcoatlus* specimens shows that the wings were eleven meters across (Langston personal communication). The biggest

Pteranodon skull indicates an eight-meter wingspan (Harkson 1966).

Protocrocodilians These small archosaurs tend to be very like protodinosaurs in design: gracile, with fairly erect limbs and digitigrade feet. Certainly their fastest gait was a bounding gallop. The wrist is bizarre because two of the proximal carpals are hyperelongated. Quite unique, this may be a way of lengthening the hand while retaining a plantigrade stance. The outer toe is extremely reduced. The reconstruction by Crush (1983) of *Terrestrisuchus gracilis* is very nice except for the sway back.

Predatory dinosaurs The first dinosaurs such as *Lagosuchus talampayensis* (Fig. 10a) were tiny predators, only a foot or so long and weighing only a tenth of a kilo. The long, flexible backs of these erect, long-limbed animals suggest that they often bounded, but their fore limbs are short enough for bipedal running too. Whether they had a divergent thumb weapon is not known. The outer toe is extremely reduced, and the toe claws are larger than in most thecodonts.

More similar to theropods are *Staurikosaurus, Herrerasaurus* (which is not a juvenile of the former), and other early predatory dinosaurs. Unlike that of true theropods, the ilium remains short and the fourth toe is still fully developed. Very short fore limbs do demonstrate full bipedality. *Herrerasaurus* is unusual in having a retroverted pubis, mimicking protobirds and ornithischians.

Theropods are a uniform group, very birdlike, fully bipedal with short trunks, long, deep narrow hips, and long, narrow, three-toed feet (Figs. 10b–14). Thousands of theropod trackways prove that they always strode, never hopped (contra Raath 1977).

I am amazed by continuing claims that theropods were mere scavengers (Halstead and Halstead 1981). Animals do not go around with 6-inch teeth and enormous jaw muscles just to pick at carcasses! Purely terrestrial scavengers are unknown; only weakly beaked and footed soaring birds can afford the enormous search time required to find dead animals (Houstan 1979). The suggestion by Welles (1984) that slender-snouted *Dilophosaurus* killed with its feet does not take into account the vomers bracing the snout or the very large teeth. The longstanding belief that theropods were aquaphobic never had any basis. Almost all animals swim well, including big ground birds, and the powerfully limbed, long-toed theropods were probably better at swimming and traversing mud flats than most dinosaurs (see Coombs 1980).

Lips probably covered the teeth when the mouth was closed. Theropod cheeks are broader than the narrow snout. Theropods did not have raptorlike orbital bars shading their eyes. However, their skulls did bear a varying array of crests and horn bosses. The nasal horn of *Ceratosaurus* is well known, *Proceratosaurus* and *Ornitholestes* (Paul, in press, c) had them too. Many other theropods had rugose nasal surfaces that supported a low horn ridge, including ornithomimids. Still others had sharply rimmed and prominent outer nasal edges enlarged by horn ridges. This was taken to an extreme in bony (not horn) crested *Dilophosaurus*. In protobirds the nasal horn sheaths may have migrated forward to form a protobeak. Virtually all theropods and protobirds had a small hornlet or boss just above and before the orbit, sometimes another just above and behind the orbit. In *Carnotaurus* these combined into a hyperenlarged horn (Bonaparte 1985).

Tarsitano (1983) suggests that theropod necks were straight, but so strong is the vertebrae's beveling that it is questionable whether they could completely straighten their necks (Osborn 1906, 1917; Gilmore 1920; Ostrom 1969; Madsen 1976). I show them in their naturally articulated or neutral S curve and the skull extended to its maximum, a rather canidlike threat posture. Normally theropods carried their necks more erect to shift the center of gravity closer to the hind limbs and improve the view of the landscape (Fig. 5). The slender, birdlike neck of small theropods must have been lightly muscled; in big species tall occipital crests imply powerful, bulldog upper-neck muscles. The base of the tail tilted up a little.

Early theropods up to *Ceratosaurus* have four fingers, of which the outer is very reduced and unclawed. Most theropods have three fingers, tyrannosaurs only two (the disarticulated and poorly

Figure 9. "*Quetzalcoatlus northropi* trio" in flapping flight. The head of an adult was about 2 meters long, and its total wingspan was some 11 meters (much of the data for this restoration is from half-sized specimens). This animal apparently had a posterior skull crest, but its form is not known; the individual with larger crest is a "male." Note that fur streamlines the fore-limb bones, muscles, and joints into the leading half of the wings. For AeroVironment version, see MacCready (1985) and Parrish (1986).

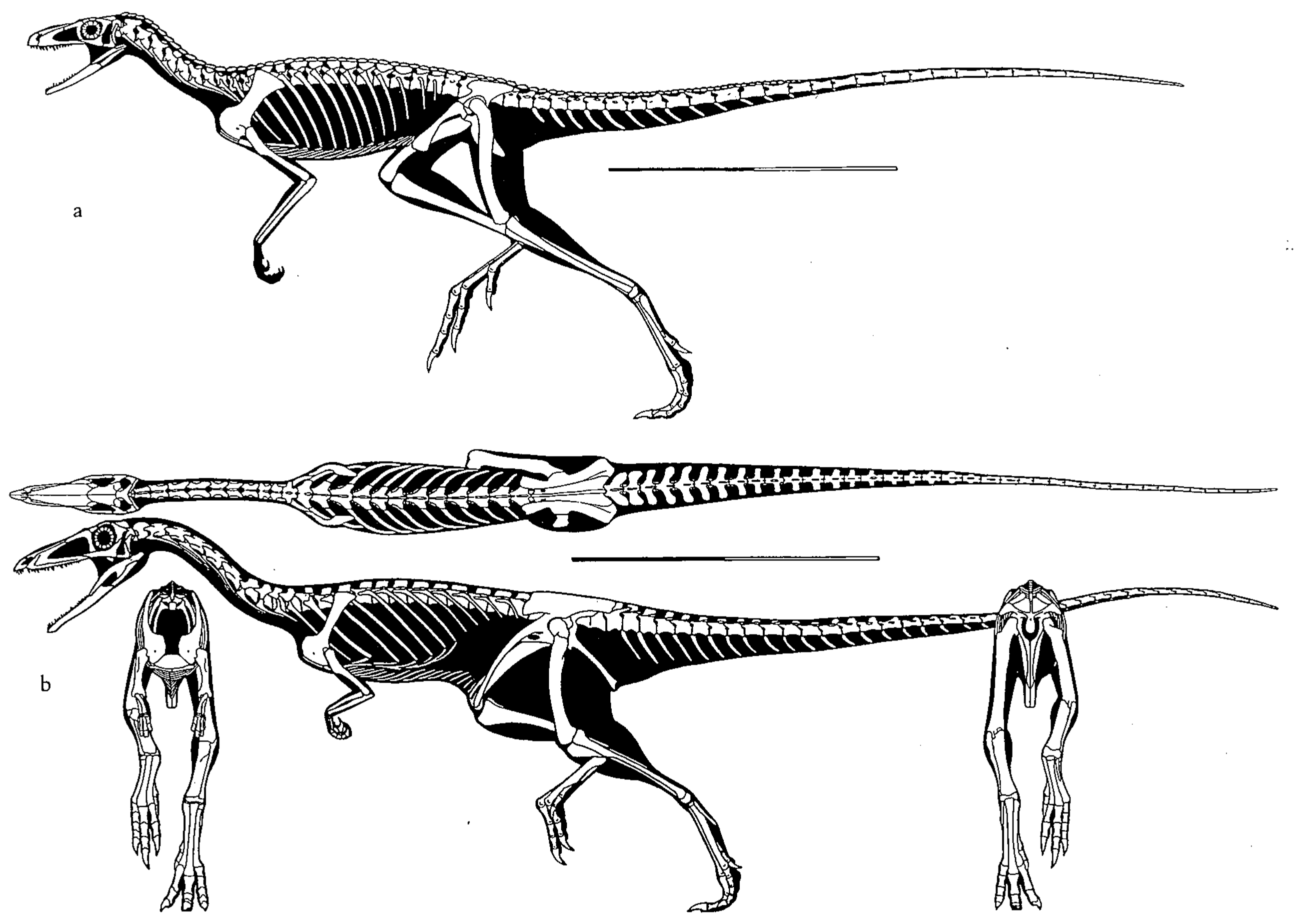


Figure 10. a. *Lagosuchus talampayensis* mainly after PVL 3870. The skull is restored in part after *Lewisuchus,* the hand is unknown; data is from Bonaparte (1971, 1975); scale bar equals 100 millimeters. Note that even this protodinosaur has an S-curved neck. b. The early theropod *Coelophysis (=Syntarsus) rhodesiensis* based primarily on holotype QG 1; scale bar equals 500 millimeters. Compare to Raath (1977), whose restoration is too long in the neck and too short in the trunk.

preserved *Compsognathus* hands do not confirm Ostrom's 1978 suggestion of two fingers).

Tarsitano (1983) argues that theropod hips must have been tilted up twenty degrees when moving, not horizontal. Actually either is possible. We cannot reconstruct and measure limb action and muscle-stretch values well enough to know. The narrow-hipped theropods waddled only a little, like narrow-hipped ground birds, not like fat-hipped ducks. The innermost hind digit is very reduced. That many articulated skeletons show this toe only partly reversed, while some trackways show it fully reversed, suggests that it was mobile. The three central toes, which are long in even the biggest species, are underlain by birdlke rows of small pads and are a little pigeon-toed. The outer digit is reduced to an ankle splint. The toe claws are smaller and blunter in allosaurs, ornithomimids, and tyrannosaurs. Hence they delivered ostrich kicks instead of bouncing on their slender tails.

I find it difficult to conceive of the very *Archaeopteryx*-like small theropods not being feathered as are their bird descendants. As for big theropods, Russell (personal communication) has found a small patch of small mosaic scales on the tail of a tyrannosaur. It is quite likely that, like birds, theropods had rows of large scales running along the upper surfaces of the feet and toes. *Ceratosaurus* has an unusual row of irregular scutes running atop its vertebral spines (Gilmore 1920). It is very unlikely that *Tyrannosaurus rex* had scutes (Osborn 1906), all other articulated tyrannosaur skeletons lack them.

It is often stated that juvenile theropods hunted independently, but since many dinosaurs were social it is likely that adult theropods took care of the juveniles, at least until partly grown.

Bidar, Demay, and Tnomel (1972), who postulate that *Compsognathus* was a webbed-handed diver, provide a treatise on how not to describe and illustrate a dinosaur. All tyrannosaurs, not just *rex,* had unusually broad cheeks and a fair degree of binocular vision, which is sometimes obscured by lateral crushing. The skull cheeks of the well-known *T. rex* at the American Museum of Natural History (AMNH 5027) are too broad due to dorso-ventral crushing, but Molnar (1973) makes them too triangular. Newman (1970) correctly shortened the tail of *T. rex,* but the disarticulated neck vertebrae and drooping foot are in error (see Paul and Chase, in press).

The protobird *Archaeopteryx lithographica* has big, fully aerodynamic, powerfully muscled fore limbs and probably flew well. It lived upon arid islands that supported only scrub (Viohl 1985); the many restorations showing it in trees are, therefore, not correct. It was a good climber, though, and may have been a shorebird that rested in shoreline foliage. Birds do not regularly hunt ultraswift dragonflies, so restorations showing protobirds engaged in such activity are not tenable.

Examination of another protobird, *Velociraptor antirrhopus,* shows that it has much the

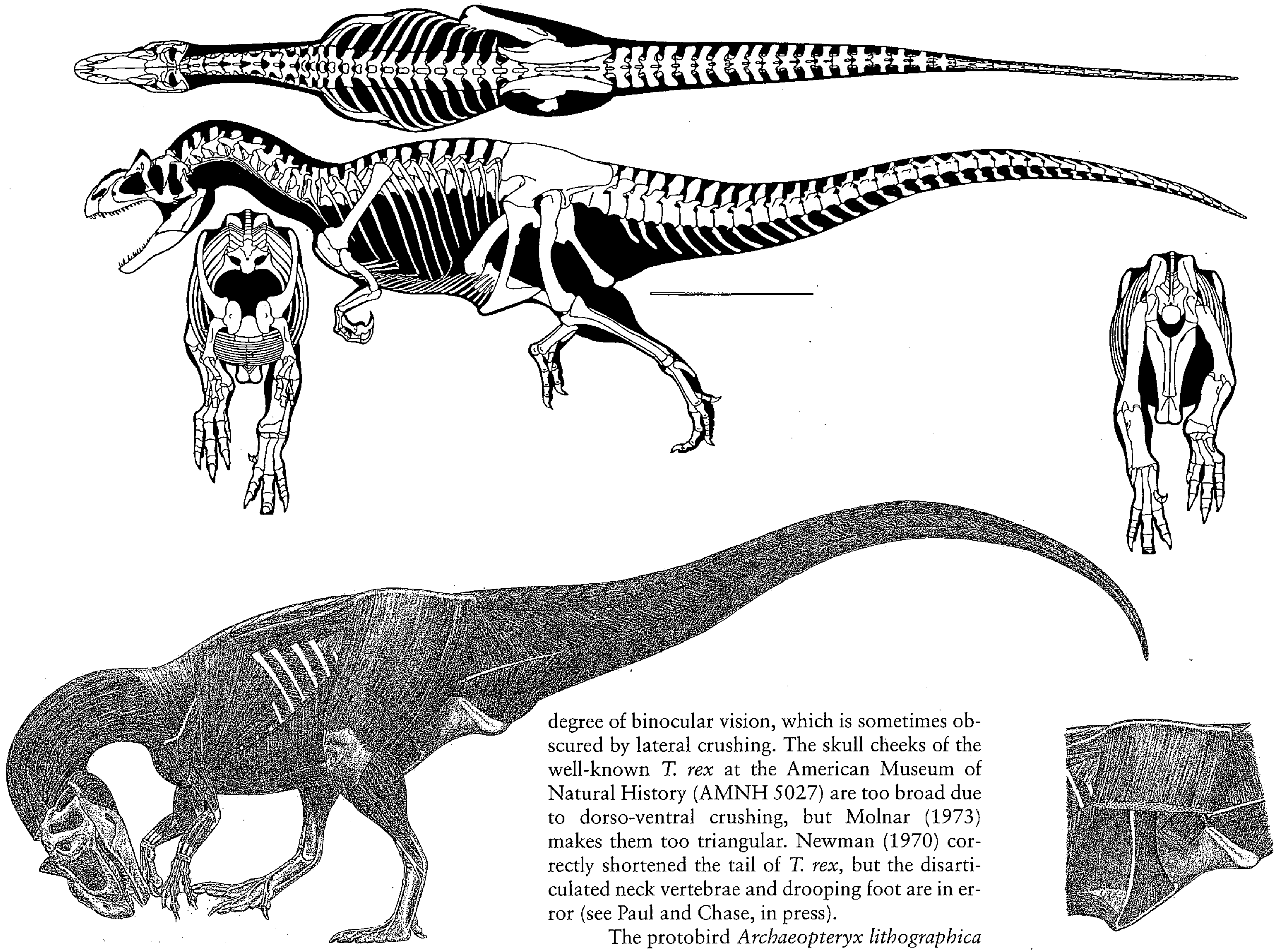


Figure 11. The first restoration of the recently mounted, nearly complete *Allosaurus fragilis,* USNM 4734; details of tail are partly from other specimens. This specimen is shorter skulled and more slenderly built than most other allosaurs. The muscle restoration shows it feeding on a carcass, the insert exposes the hip musculature. Scale bar equals 1 meter.

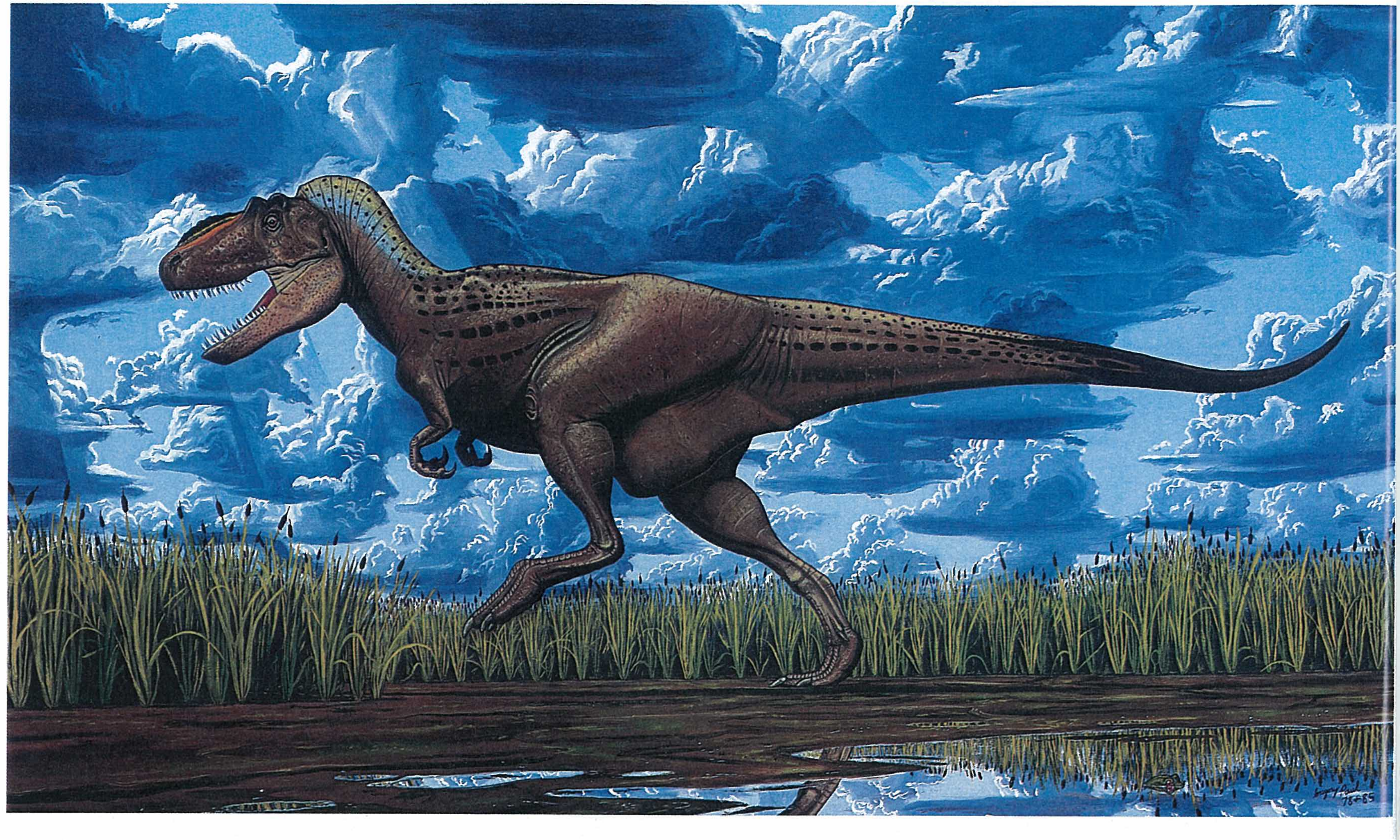
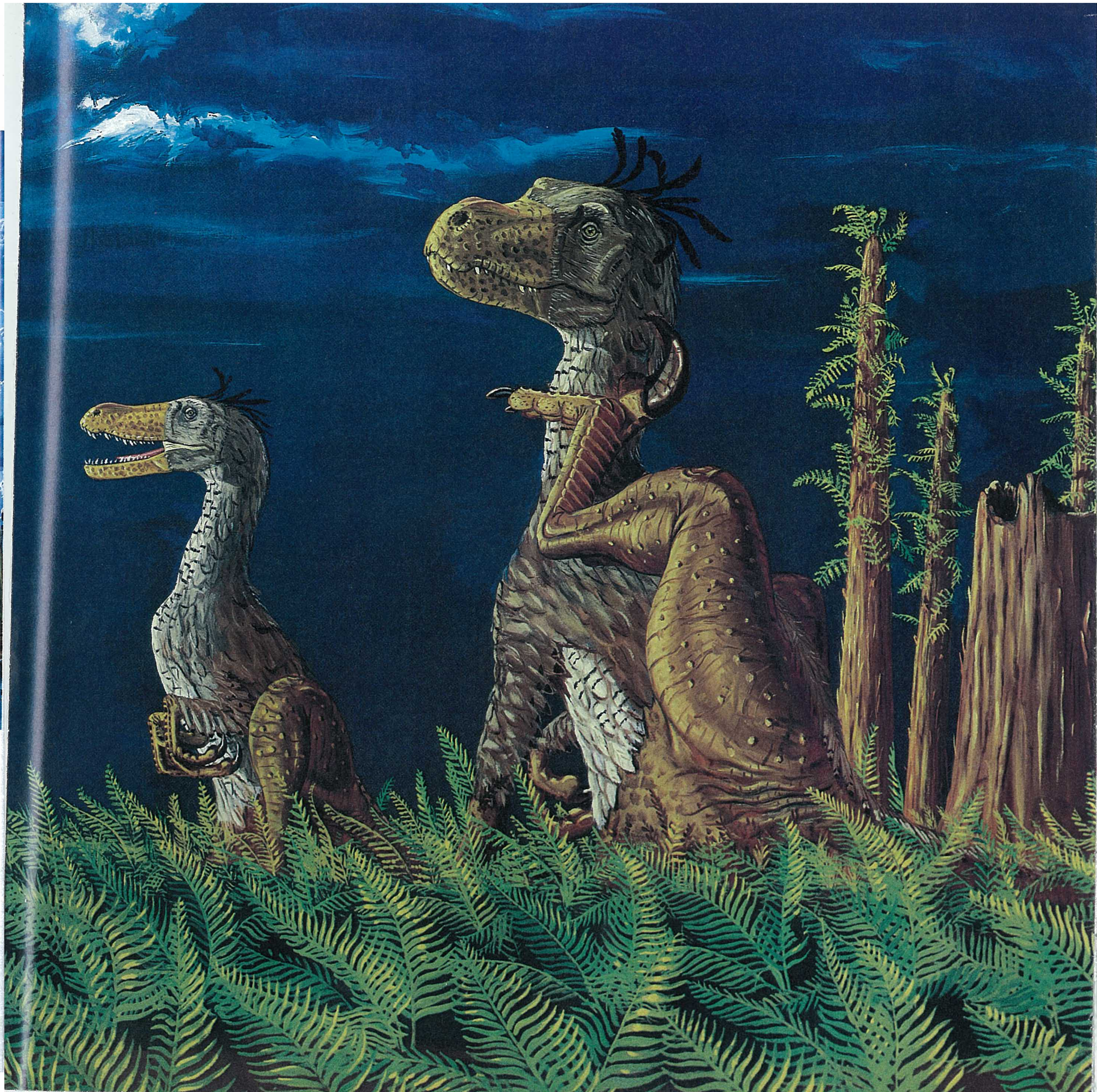


Figure 12. "*Tyrannosaurus (Daspletosaurus) torosus* in a Fast Run." The power of the skull and hind limb are emphasized at the expense of the fore limbs. The locale is a cattail marsh in the Judith River. This painting has been extensively modified (the original version is reproduced in Paul 1984b). Checklist 84.

same large, low head with an upturned snout as *Velociraptor mongoliensis* (Figs. 13–14; Paul, in press, c; Barsbold 1983). These share with *Archaeopteryx* long, highly retroverted pubes that project behind the short ischia and ventral-caudal muscles that connect directly to the pubis as in birds. The restoration of *Saurornithoides (= Stenonychosaurus) inequalis* by Russell and Seguin (1982) is too broad in the posterior skull (Currie 1985) and too slender in the hips and hind-limb muscles. Barsbold (1983) has shown that *Oviraptor mongoliensis* skulls had a strange nasal prominence.

The ostrich-mimic ornithomimids are usually restored with straight-edged beaks or with a sharply upturned beak tip (Osmolska, Roniewicz, and Barsbold 1972). Actually all ornithomimids share fluted upper beaks with a prominent maxillary flute, a slightly downturned, squared-off tip, and a curved lower beak tip.

Herbivorous dinosaurs Cooper (1980) contends that prosauropod hands were unsuitable for locomotion, but all known prosauropod trackways show these herbivorous dinosaurs walking on all fours (Baird 1980; Olsen and Galton 1984). Pro-



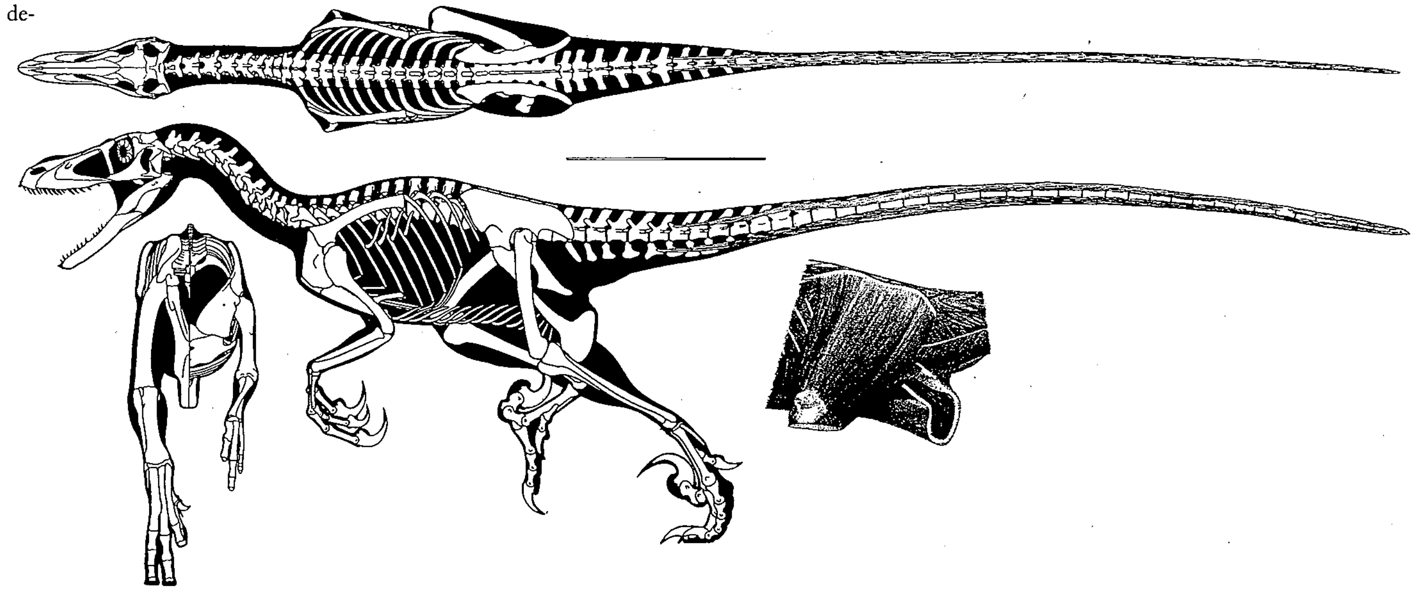


Figure 14. The protobird *Velociraptor* (= *Deinonychus*) *antirrhopus*, AMNH 3015 with skull based on YPM 5232; data is in part from Ostrom (1969), the sternal plate is from Barsbold (1983). Insert shows the hip musculature. Note the long, upcurved skull, the forward-facing eyes with binocular vision, and the great sickle claw. The tail could bend up 90 degrees at its base. Scale bar equals 500 millimeters.

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Figure 13. "Resting *Velociraptor antirrhopus* Pair." Most big predators spend most of their time relaxing and sleeping while digesting their last meal. This pair is getting hungry, as shown by their hollow bellies. These protobirds are shown insulated in feathers. Note the various horn ridges on the head and the protobeak. Only the tips of the teeth show beneath the upper lip. The locale is the Cloverly Formation; the flora consists of ground ferns and the bizarre tree fern *Tempskya*, its fronds blowing in the wind of an oncoming storm. Checklist 83.

sauropods have among the longest and most flexible backs of dinosaurs, and they retained a primitive bounding gallop (Fig. 15). As Bakker (1978) notes, prosauropods probably reared high to browse.

Heavily built, shortfooted prosauropods such as *Euskelosaurus* (= *Melanorosaurus, Riojasaurus*) were the ancestors of sauropods. The more complex vertebral articulations and shorter hind feet suggest that they galloped less and trotted more. Measurements of a *Euskelosaurus* hand and foot by Ellenberger and Ginsberg (1966) must be reversed because as presented the hind feet are absurdly tiny and the hands enormous. Prosauropods have five free fingers, of which only the inner three bear claws. The slightly outward-facing hind feet are four-toed, each with a large claw and small pads.

Prosauropods were beginning to develop cheeks at the back of their mouths (Paul 1984b). Slender birdlike necks and small skulls suggest light muscles. Galton (1985) shows that prosauropods were herbivores, not predators as suggested by Cooper (1980) and others. It is important to note that all reports of blade toothed prosauropods and sauropods are due to false associations with the shed teeth or fragmentary jaws of truly predatory archosaurs.

Despite the great difficulties in excavating sauropods, a surprising array of new species based on very good skeletons has recently been uncovered on four continents. That their skeletons continue to be mounted incorrectly shows that they are in need of a structural reappraisal. Riggs (1904) and Bakker (1971b, c) show that sauropods were terrestrial, a view that appears almost universally accepted (excepting Halstead and Halstead 1981). Indeed they preferred seasonally dry, open conifer-cycadeoid woodlands where they browsed among the tree crowns (Bakker 1971b, c; Dodson, Behrensmeyer, and Bakker 1980). The incompletely straight knee and ankle of the very early *Vulcanodon* suggest that it was a little faster than the others.

Coomb's suggestion (1975) that sauropods had proboscides is unlikely because of the lack of appropriate facial muscles, the absence of scars for these muscles, and the weakness of the nasal bar in some species. Furthermore, sauropod jaws and teeth are well-worn, strong, powerfully muscled cropping organs that did, I believe, not need the assistance of a trunk. Because their mouths were for cropping, not chewing, sauropods lost all traces of cheeks.

Many sauropods had erect, S-curved necks. Diplodocids differ in that the neck was straighter and more horizontal (contra Knight in Massey-Czerkas and Glut 1982: 38, 43; Watson and Zallinger 1960; Bakker in Crompton 1968, and personal communication). Since sauropod skulls were small and the neck vertebrae are very like those of long-necked birds, their necks were lightly muscled. *Brachiosaurus brancai* (Fig. 17) is quite unusual in having withers—tall neural spines over the shoul-

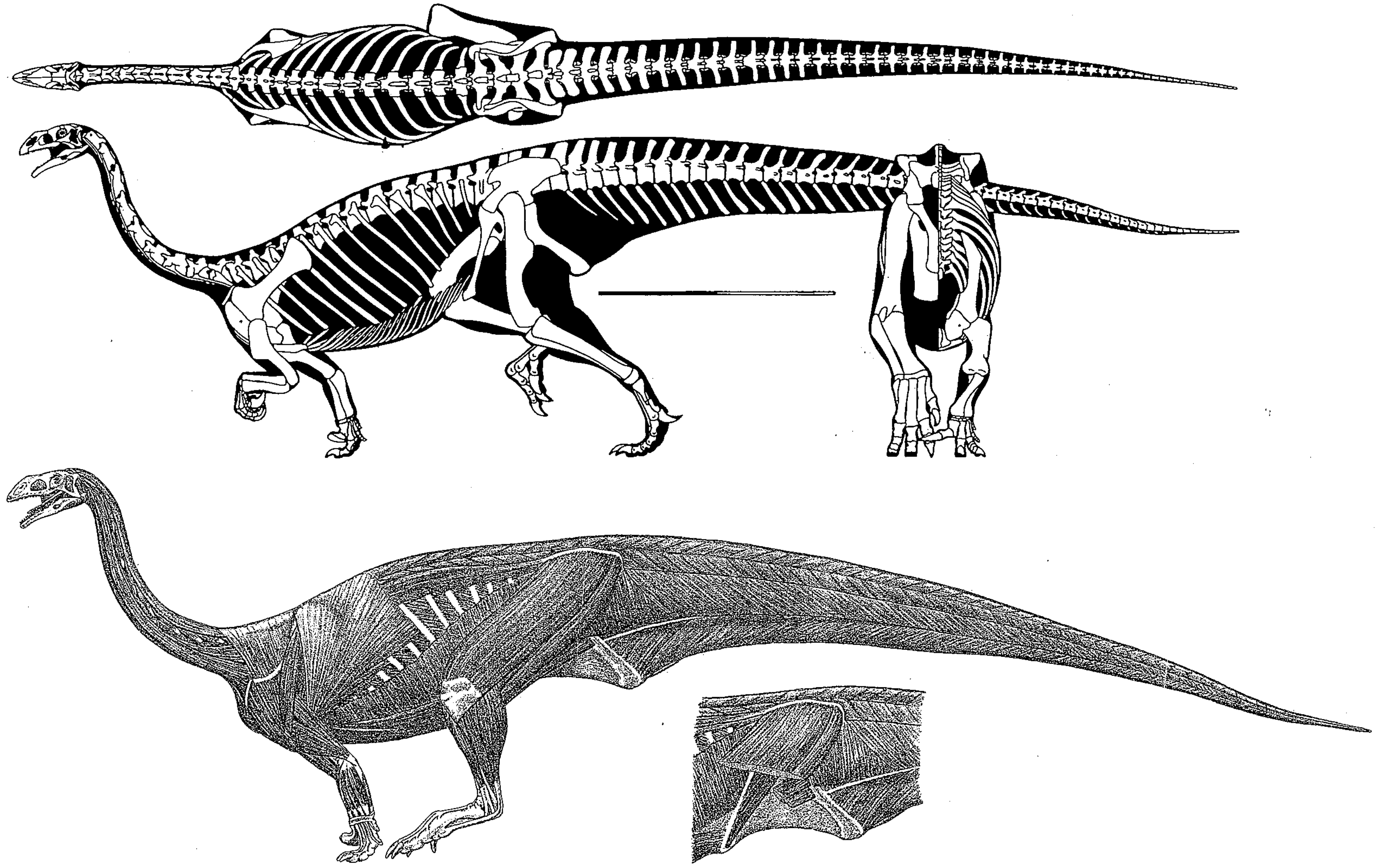


Figure 15. *Plateosaurus engelhardti*, HMN XXV, with skull based on AMNH 6810; data are from Huene (1932). Prosauropods are the only dinosaurs that retain both the clavicle and interclavicle, but they are not connected. The muscle restoration shows the dinosaur in a bounding gallop, the insert exposes the hip musculature. Scale bar equals 1 meter.

ders—that may have supported a set of low camellike nuchal ligaments. Brachiosaurs and many sauropods retain single neural spines, but advanced diplodocids and camarasaurs are famous for their V-shaped neck spines. That a cable ligament lay between these spines is unlikely because it would have had little leverage in this position. Alexander's calculations (1985) that sauropod neck-lifting ligaments and muscles projected well above the neural spines ignore the tissues between and astride the spines. Instead the space between the V spines may have been partly hollow.

The base of all sauropod tail vertebrae articulates in an upward arch (Gilmore 1932, 1936). Lacking any leverage, the whiplash vertebrae of diplodocids must have drooped from the fleshy section of the tail.

Riggs (1904) and Bakker (1971c, 1978) are almost certainly correct in arguing that, like giant ground sloths, diplodocids reared into a tripodal stance to feed or fight. It is the only explanation for their extremely massive hips and associated vertebrae, since other, bigger sauropods have much smaller hips and posterior vertebrae. Rearing also explains the diplodocid's straight necks, short fore limbs, and sledlike chevrons. All sauropods, even *Brachiosaurus,* however, bore most of their mass on their more robust hind limbs and could rear on occasion. Sauropod-theropod combat must have been impressive (Fig. 16).

This is confirmed by the divergent, bigclawed thumb weapons of diplodocids, which are separate from the main united finger unit. Camarasaur and brachiosaur thumbs are not separate and are much smaller. The rest of the hand digits are extraordinarily reduced and short in sauropods; not even hooves were present. Very odd is the rarity of thumb prints in fore prints (Bird 1944, 1985; Lockley, this book) although at least one thumbclaw print is reported by Ginsberg et al. (1966). Some shallow prints can be attributed to diplodocids walking with thumb claws clear of the ground, but not the deep ones.

Sauropod hind limbs, always stouter than their fore limbs, were laterally broad but anteroposteriorly slender compared to those of elephants. The plantigrade hind feet in Cooper's sauropod re-

Figure 16. "Ambush at Como Creek: *Allosaurus atrox* Pack Versus a *Diplodocus carnegii* Herd," an example of what combat between big theropods and sauropods may have been like. Note that the diplodocid herd is retreating onto firm ground as two adults protect a juvenile. Locale is the famous Como Bluff quarry in Wyoming, Morrison Formation. Araucarian and other conifers, cycadioids, and ferns make up the rather dry adapted flora. This painting has been substantially modified (an earlier version is reproduced in Bird [1985] and Czerkas [1986]). Checklist 89.

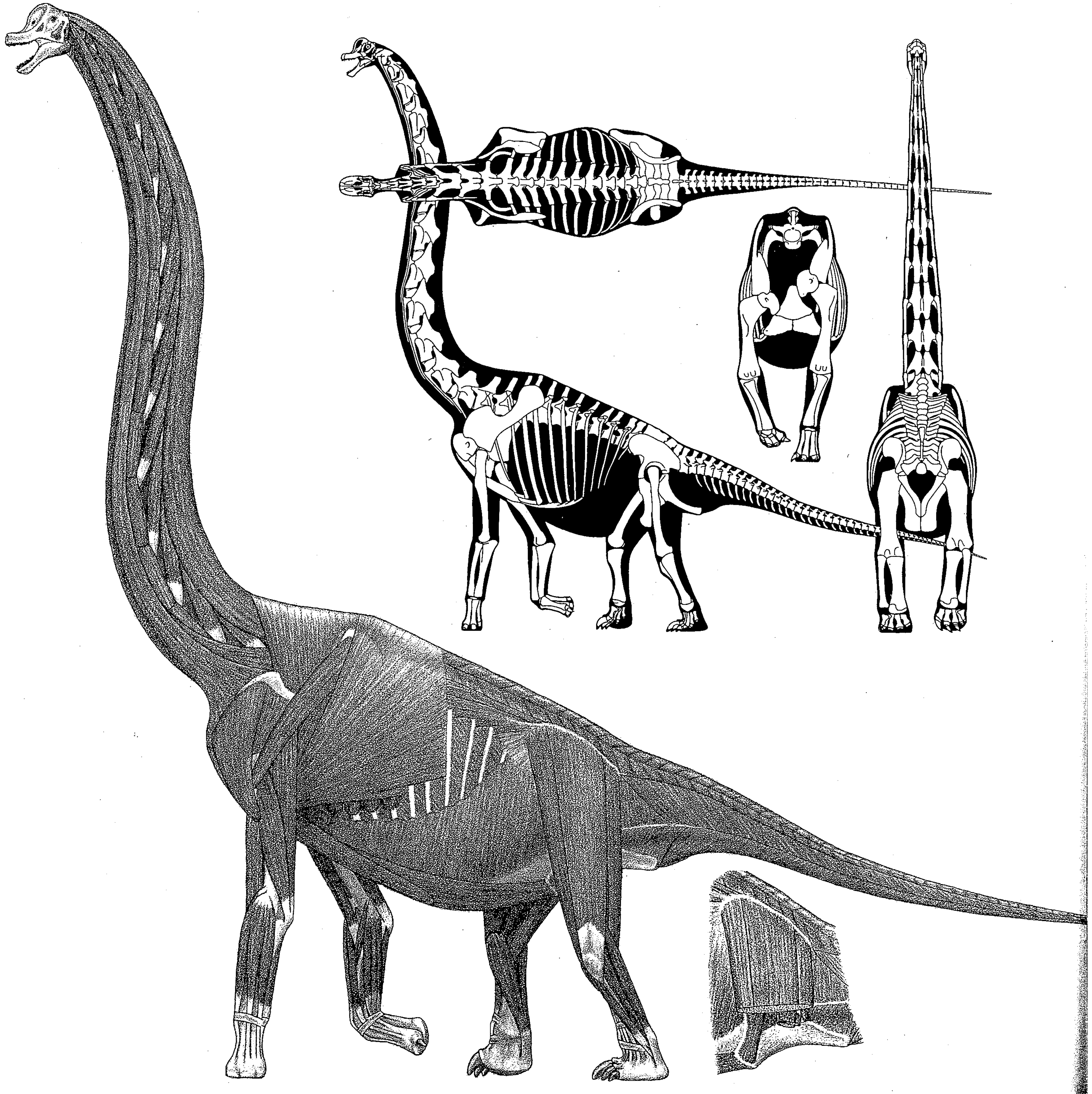


Figure 17. *Brachiosaurus brancai,* HMN SII, with most of posterior column, hips, and hind limbs after other specimens; compare to Janensch (1950a). Note the withers formed by tall shoulder spines—only chasmosaurs (Fig. 23) also have this. Insert exposes the hip musculature.

construction (1984) resulted from a misarticulated astragulus and incomplete tibia. In well-preserved sauropod ankles the astragulus is actually rotated backward relative to that of prosauropods (Janensch 1961: pl. XXI), giving them elephant-style, unguligrade hind feet. They are also rather like African elephants in the absence of hooves on two of the toes; but unlike elephants in that the inner three or four toes bear increasingly massive banana-shaped claws that sweep down and outward (Hatcher 1901; Bird 1944; Ginsberg et al. 1966). Theropods approaching the hips of sauropods were in danger of receiving a nasty kick!

Because they are so reminiscent of elephants it is tempting to restore sauropods with thick, wrinkled skin. Small patches of skin impressions, however, show a thin, unwrinkled skin of very small bead scales, which could not have been seen from more than a few meters away. It appears that a few species may have been lightly armored (Powell 1980), but this is not yet completely certain.

Burian's well-known restoration of *Brachiosaurus brancai* (Spinar and Burian 1972) is faulty in almost all respects, including being posed in an unnatural gorge lake. My new restoration (Paul, in press, b: fig. 24a) shows that *B. brancai* is shorter trunked and more gracile than previously realized. The largest *B. brancai* specimens are similar in size to "Ultrasaurus."

Many of the new Chinese sauropods appear to represent a radiation of basal diplodocids. He et al. (1984) note that *Omeisaurus* and *Mamenchisaurus* are close relatives. Therefore the skull of *Omeisaurus,* instead of the skull of *Diplodocus,* should be used to restore the unknown head of *Mamenchisaurus*. Watson and Zallinger (1960) and Zallinger (1977) persist in restoring *Apatosaurus* with the overly long plaster fore limbs of the AMNH mount (a good example of why one must be sure to determine what is real and not in skeletons!).

I find the elephantine sauropods among the most elegant and majestic of all creatures.

Ornithischians are characterized by beaks, cheeks covering the sides of the mouth (Galton 1973), and retroverted pubes. Horn lengthened the beaks. Tyson (1977) shows that the cheek was probably a pinnate muscle that formed a gentle contour as it rose from under the jugal. Even the most primitive species, including *Lesothosaurus,* had them (Paul 1984a). The ribs tend to bunch closer together at their lower ends than in other dinosaurs. Note that the posterior ribs were always in front of the prepubis, never outside it.

Having beaks, cheeks, and retroverted pubes, segnosaurs can be considered basal ornithopods (Paul 1984a); certainly they are not theropods. No single good specimen exists, so parts from various segnosaurs must be used for a composite restoration (Fig. 18a). *Nanshungisaurus,* published as a small sauropod (Dong 1979), is a segnosaur. Enormous-clawed *Therizanosaurus,* published as a theropod, has a remarkably segnosaurlike scapulacoracoid and humerus. These rather prosauropodlike quadrupeds have four-toed feet with remarkably big claws. The anterior iliac blade flares outward an incredible amount and supports an enormous gut.

The long, strong fore limbs of these early, yet sophisticated and gracile ornithischians suggest that heterodontosaurs were quadrupedal gallopers. The best-articulated skeleton clearly shows a strong downward arch (Fig. 18b; contra Santa-Luca 1980). This skeleton also has inwardly divergent thumbs as per Bakker and Galton (1974), and their restoration of the hand is more accurate than Santa-Luca's. The five-fingered hand bears three inner claws, the four toes a claw each.

Scelidosaurus (Fig. 19a) and *Scutellosaurus* are primitive, quadrupedal ornithischians that lack the skeletal specializations of stegosaurs and ankylosaurs, but have extensive armor coverings. Indeed the body form is so standard that there is little that needs to be said about it. *Scelidosaurus* has normal dinosaur skin (Norman 1985). The hands are not known, the feet have four-clawed toes.

With the anterior dorsal ribs swept back, the shoulder girdle of the stegosaur is set far back, so that they have long, slender, S-curved necks instead of the short, stout, straight one seen in most restorations. The tail base is upwardly arched.

Bakker (1971c, 1978) is probably correct in suggesting that stegosaurs reared to feed, using their surprisingly diplodocidlike tails as a prop. Of

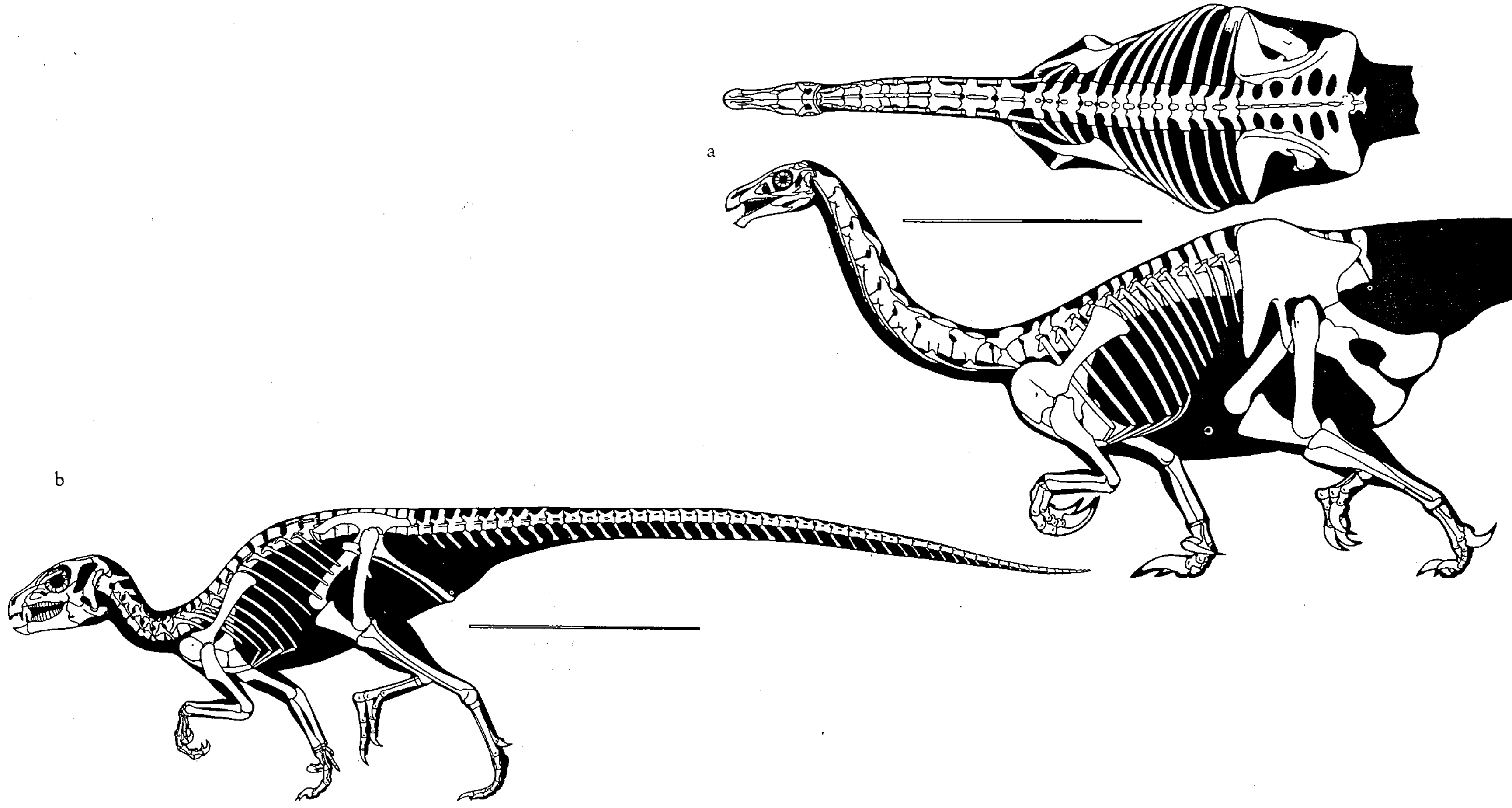


Figure 18. Basal ornithischians. a. A composite segnosaur based mainly on *Nanshungisaurus brevispinus* presacrals and hips, and *Erlikosaurus andrewsi* skull (information on the tail has not been published). Proportions are approximate; scale bar equals 1 meter. b. The nearly complete *Heterodontosaurus tucki*, SAM K1332. Scale bar equals 250 millimeters. Data from Santa-Luca (1980) and Barsbold (1983).

course, their tails were also powerful weapons.

The small, early stegosaur *Huayangosaurus* is only partly rectigrade in limb design, and unlike other stegosaurs it could probably still trot. Stegosaur hands and feet are exceptionally short and small, with only three toes. The digits themselves are exceptionally short. The inner two fingers have flat hooves (Sereno personal communication), the outer three are buried. There are only three toes; these have blunt, vertical, rather elephantlike hooves and were backed by a large elephantine hind pad.

Small armor nodules encase the neck (obviously this slender organ was a tempting target). The great plates and horns were much enlarged by horn sheaths and not skin alone as implied by Buffrenil, Farlow, and de Ricqlès (1984). Bakker (in Wood et al. 1972) suggests that the plates, except the broad-based front and back plates, were mobile. A pair of virtually identical plates in the holotype *Stegosaurus ungulatus* (YPM 1853, Ostrom and McIntosh 1966: pls. 59–1, 60) suggests that the plates were paired, but other arrangements are possible (Czerkas, this book). In *S. stenops* the s-curved tail tip and differentially beveled spike bases caused the spikes to diverge from each other like a pincushion (Fig. 20b; Ostrom and McIntosh 1966: pl. 54). Some stegosaurs appear to lack this adaptation (Dong, Zhou, and Zhang 1983: fig. 102).

Most stegosaurs are like other ornithischians in being fairly long and low. *Stegosaurus stenops* (Fig. 19b) proves to be about as tall and short as *S. ungulatus*. But Lull's *S. ungulatus* restoration (1910), based on different-sized specimens, is too short. *S. stenops* has exceptionally large plates; *S. ungulatus* has four or more pairs of tail spines to the former's two.

The idea that these very elephantine animals rolled up like hedgehogs for protection (Ratkevich 1976; McLoughlin 1979) is best characterized as ludicrous.

Carpenter (1982, 1984) has done crucial work on the difficult problem of reconstructing the skeletons and armor of ankylosaurs and nodosaurs. I have not attempted a skeletal reconstruction because of unresolved design question. Coombs (1979, personal communication) and Huene (1956) indicate that ankylosaurs have twenty-four to twenty-six presacral vertebrae, Carpenter and Nopsca (1928) suggest twenty. In addition, some ankylosaur and nodosaur pelves are incredibly broad, and personal inspection revealed no strong dorso-ventral crushing. But other specimens (especially British Museum (Natural History), BMNH 5161) and Carpenter (1984) suggest narrower pelves. It is particularly difficult to resolve the greatly differing lengths of the sacralized dorsal ribs in various specimens and reconstructions.

Ankylosaurs are unusual among dinosaurs in having relatively small eyes. The tail base is directed downward, but the tail does not drag on the ground (Carpenter 1982, 1984). The idea of Wood et al. (1972) that ankylosaurs were made primarily of "solid fat" is due to a misunderstanding about their great girth (Bakker personal communication).

The fusion of a scapulacoracoid to a rib in one specimen (Maryanska 1977) is difficult to confirm. If correct, it is either a pathological or a secondary restriction of scapular mobility. The nodosaur's vertical fore limbs are evidence of a slow gait. The hind-limb-dominant nodosaurs, however, have short fibulas (Coombs 1979: fig. 5d–e) so that the knee appears to have been flexed and the ankle was mobile. This condition is intriguing because it is similar to but the reverse of that seen in fore-limb-dominant camels, which have straight knees and flexed elbows (Muybridge [1887] 1957). Apparently these animals have kept their strongest limbs flexed for trotting and slow galloping. The stronger-limbed, completely flex-jointed ankylosaurs were probably full gallopers. They have five free fingers, of which the inner three or four appear to have had small hooves. Trackways show that the slightly outward facing hind feet were backed by a fairly large, rhinolike pad. The four toes were separate and bore well-developed hooves.

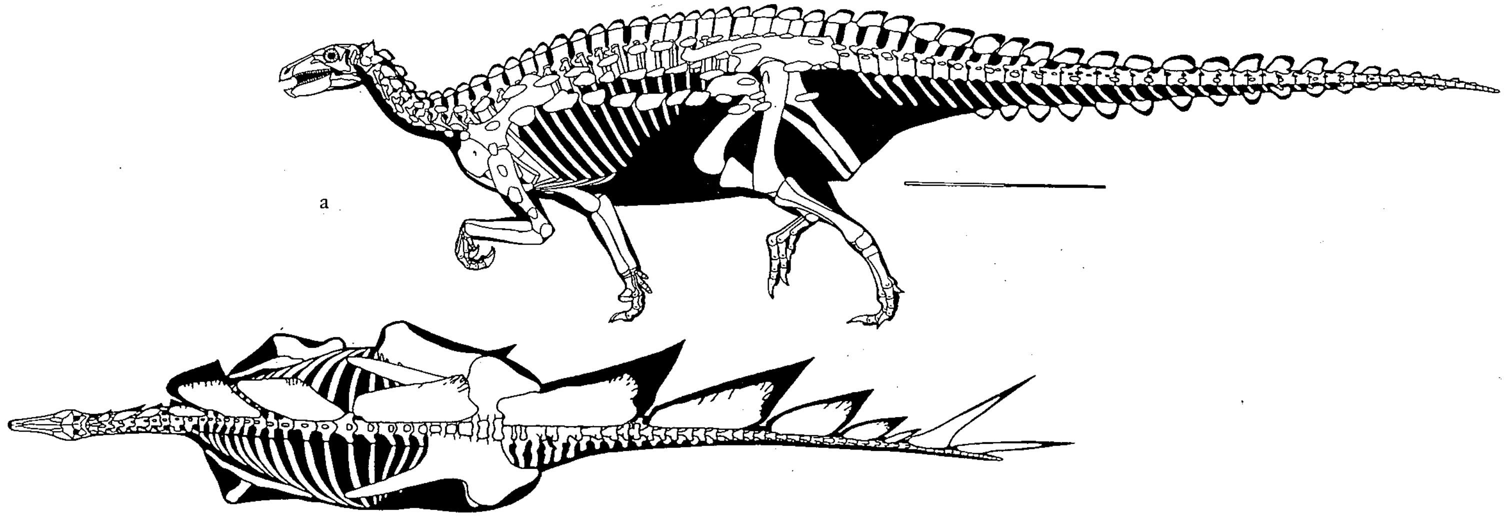
When the body proportions are pinned down, the remains of articulated armor and impressions of skin make these among the most restorable of dinosaurs.

Pachycephalosaurs are among the most bizarre of dinosaurs and the only ones more interesting in top view than in side view (Fig. 20). This is because of their incredibly broad ribcages and unbelievably long tail-base transverse processes. No other dinosaur has anything like the latter. The absence of anterior chevrons is another peculiarity. The unusually spacious tail base must have supported an unprecedented migration of part of the digestive tract to behind the hips (Bakker, this book). That the neck is unknown is unfortunate since it may have been specialized to absorb the stress of using the dome-roofed skull as a battering weapon. The tail base is down-arched a little, and its end is stiffened by a crisscross of ossified rods. The hands are unknown, the four-toed hind limbs are like those of ornithopods.

Psittacosaurs are rather like small ornithopods in overall design. Fairly long fore limbs suggest they were at least partly quadrupedal trotters or gallopers. The jugals form very prominent cheek bosses that project out behind the narrow but deep parrot beak. The hand has four small fingers of which the outer is very reduced and the inner three have small blunt hooflets. The foot has four blunt-clawed toes of which the inner is short.

Several researchers (Bakker 1968; Russell 1970b; Coombs 1978) have suggested that protoceratopsians ran bipedally. Since scapular rotation makes the fore limbs as long as the hind limbs there is, however, no good reason for dinosaurs with such heavy heads and necks (including *Microceratops)* not to have used them. The fastest gait of the stiff-backed protoceratopsids and the big ceratopsids was probably a fairly smooth, asymmetrical, rhinolike gallop (Fig. 21).

Despite the ceratopsians' very large heads, the hind limbs are the more robust and bear most of the weight. Their trunk is also short, so ceratopsians could rear. After all, horses, bighorn sheep, takin, and elephants rear even though they are fore-limb dominant. Ceratopsians may have reared to reach the occasional choice food item or—like an enraged bear—to present a most intimidating visage to rivals and tyrannosaurs (Fig. 22). It is unlikely that horned dinosaurs relied on defensive rings. This is a specialty of open-tundra musk oxen (Nowak and Paradiso 1983), which spot predators



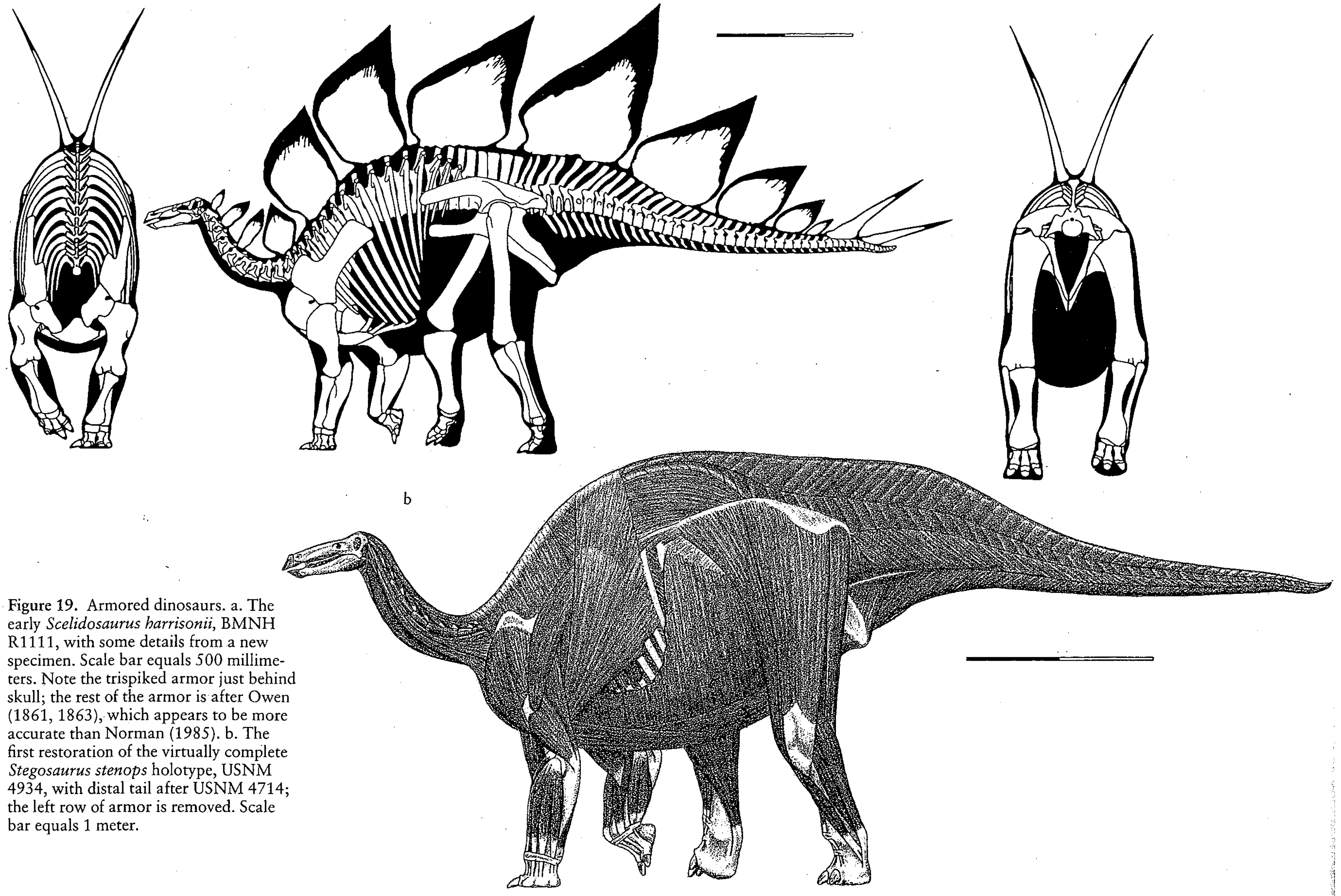
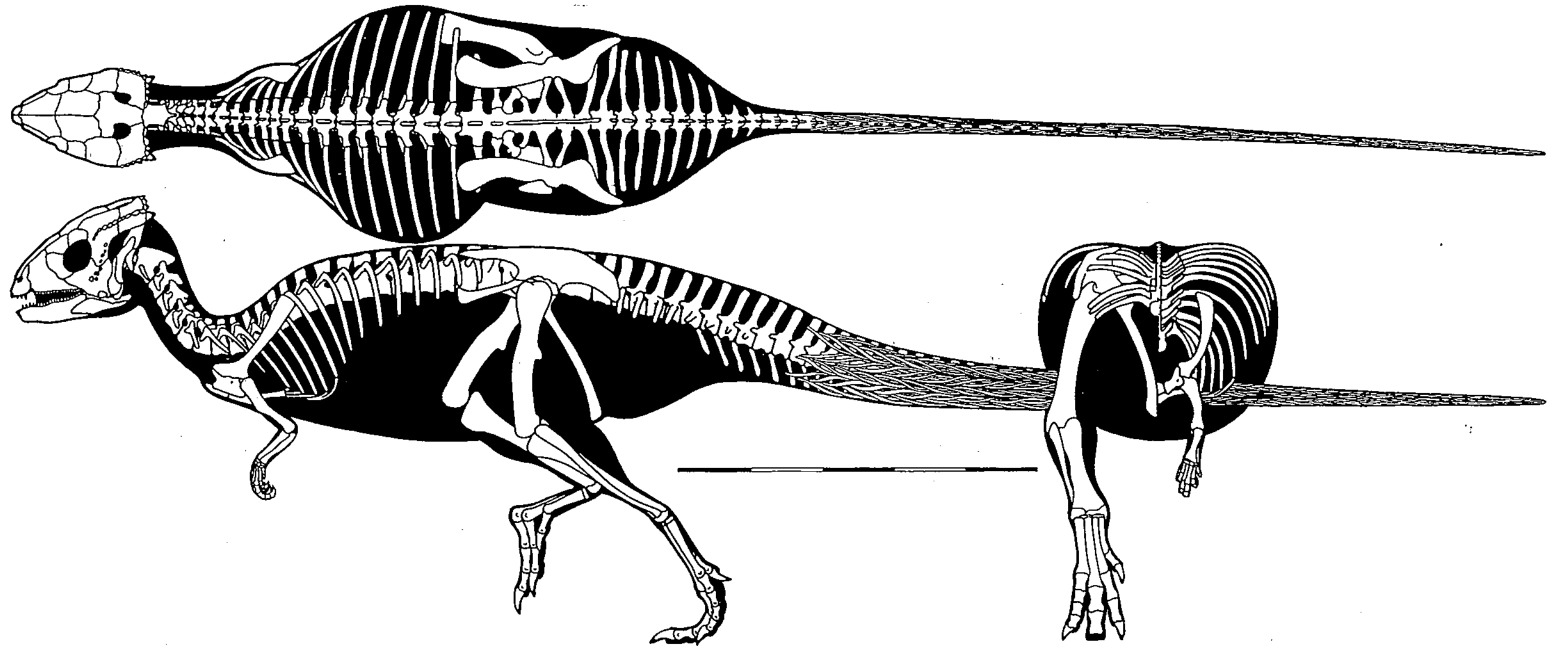


Figure 19. Armored dinosaurs. a. The early *Scelidosaurus harrisonii*, BMNH R1111, with some details from a new specimen. Scale bar equals 500 millimeters. Note the trispiked armor just behind skull; the rest of the armor is after Owen (1861, 1863), which appears to be more accurate than Norman (1985). b. The first restoration of the virtually complete *Stegosaurus stenops* holotype, USNM 4934, with distal tail after USNM 4714; the left row of armor is removed. Scale bar equals 1 meter.



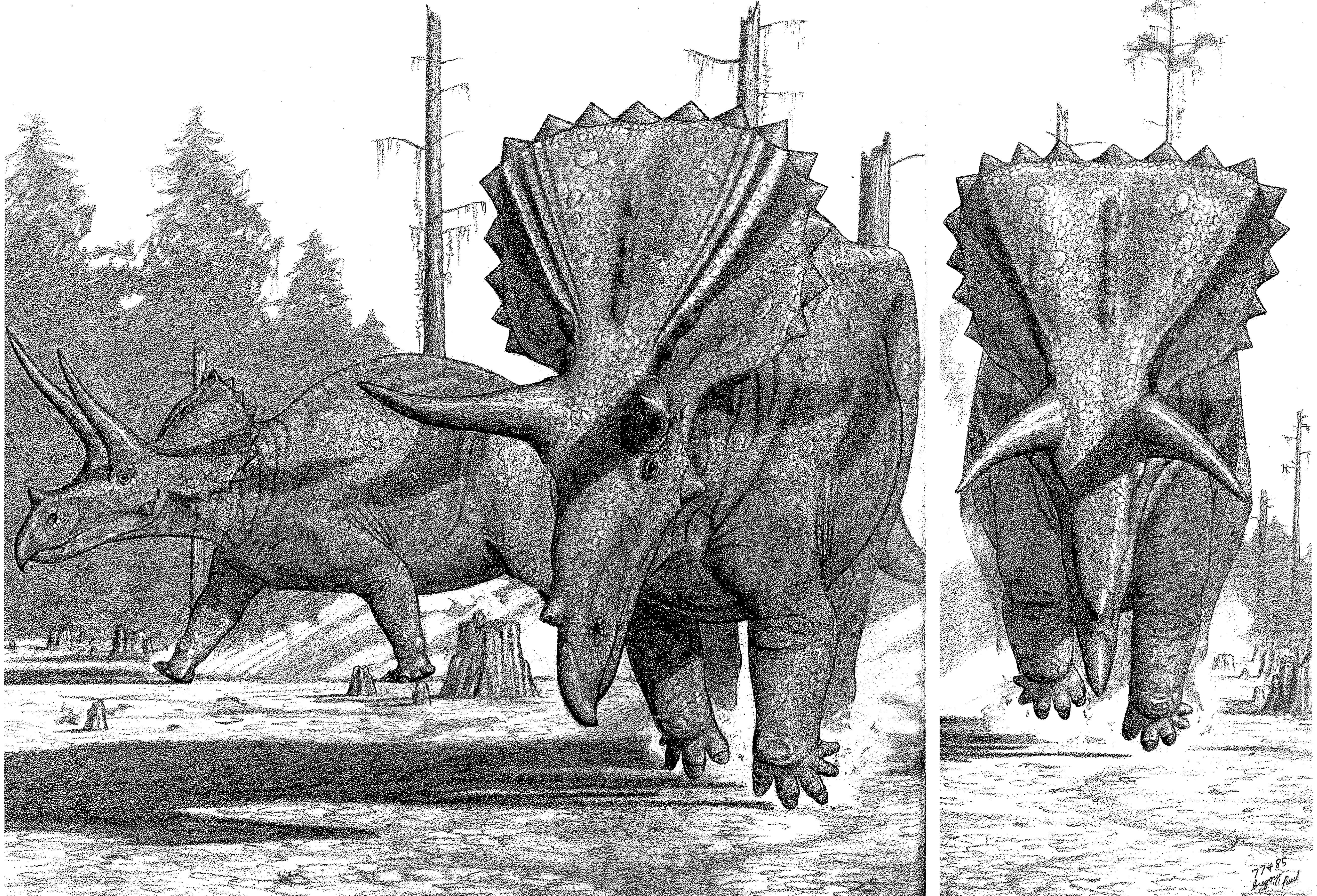
at great distances. Ceratopsians lived in wooded habitats (Russell 1977) that may have prevented them from organizing defensive rings. Their best defense was probably aggressive charging or flight into dense bush.

The restoration of the styracosaur beak by Spinar and Burian (1972), which is much too broad, has been faithfully copied by many other artists! An array of hornlets and bosses decorates the frill rim, midline, squamosal upper surface, jugal tip, and sometimes the area in front of the nasal horn. Care should be taken to apply the proper number of these elements in each species. Horn undoubtedly emphasized their appearance in life (Figs. 1, 21–23), especially in styracosaurs. In ungulates horn sheaths add from a third to double the length of the bone core; a middle value is best used for ceratopsian horns.

Rowe, Colbert, and Nations (1981) show the actual shape of the *Chasmosaurus (Pentaceratops) sternbergi* frill, and *C. russeli* has a similar frill (Sternberg 1940). It has long been argued that the frill anchored the great closing muscles of the jaw. This is the only good explanation for the great bone structure (see Fig. 1). All other big-headed animals lack such a structure, so it was not needed to counterbalance the skull as Tyson argues (1977). Display could be handled by soft tissues, so this was only a secondary function (Pringle 1978: cover). Finally in some chameleon specimens the surfaces of the frill bearing the jaw muscle are highly channeled as in ceratopsids (contra Tyson [1977]). If the suprafenestral horns of *Monoclonius* and *Anchiceratops* are the ossified cartilagenous spurs of a pinnate frill muscle they indicate that the muscle was a fairly robust belly instead of a thin sheet. Ceratopsids had wickedly powerful bites, and short-horned chasmosaurs probably bit at predators like the big-incisored Asian rhinos.

The head articulates with the neck via a highly mobile ball-and-socket joint. The neck is gently curved upward, not straight as per Lull (1933). Because the anterior dorsal ribs are swept back and the shoulder girdle is set aft, the neck is longer than usually shown. Tyson (1977) shows that the neck muscles attached to the braincase in the normal manner, not to the top of the frill as in Ratkevich (1976) and McLoughlin (1979). Hip and tail orientation is very variable, with the tail eventually directed downward (Fig. 23). The posterior dorsal ribs are strongly curved fore and aft (specimens seeming to show otherwise are partly

Figure 20. The first modern restoration of a "domehead," *Homocephale calathocercos* holotype, GI 100/51, with the neck restored and fore limbs and some other details after *Stegoceras*. The anterior caudals with their hyperelongated transverse processes are included in the posterior view. Data in part from Maryanska and Osmolska (1974). Scale bar equals 500 millimeters.



disarticulated), and one of these ribs was connected in life to the tip of the prepubis (Fig. 23; Osborn 1933).

The five fingers and four toes of protoceratopsids and ceratopsids are all free, finger 5 and toe 1 are much shorter than the others. The fingers and toes bear fairly large, flat hooves, except as usual the hoofless outer two fingers. The hind feet were probably backed by a fairly large, rhinolike pad.

Although rhinolike in body form, large skin patches show that ceratopsid skin is a very "reptilian": mosaic of large polygonal scales surrounding even larger polygonal scales (B. Brown 1917; Lull 1933). Combined with the horns, hornlets, and bosses, these large scales presented a very rich topography (Bakker in Crompton 1968; Figs. 1, 21–23). Unconfirmed is a possible row of scutes atop the tail (B. Brown 1917).

Both the largest and most uniform of the ornithischian groups, ornithopods are very important because some species can be restored with exceptionally high accuracy.

Ornithopods, except hadrosaurs, have orbital bars above the eyes that gave these most unfierce of herbivores threatening "eagle eyes." The bar is fixed to the postorbital in some species, and so it was immobile.

Many ornithopods have normally arched backs. Hadrosaurs, *Ouranosaurus, Tenontosaurus,* and *Othnielia* (= *Yandusaurus*?), however, have very strongly down-arched anterior dorsal columns (Figs. 24–26; Bakker 1978; Maryanska and Osmolska 1984). Almost all specimens are preserved this way, and straightening the back violates the anatomy. Straight-backed ornithopods were probably medium-level browsers. The down-arched backs of other ornithopods suggest a preference for browsing ground cover, and this is confirmed by their broader, more rectangular beaks (Figs. 24, 26).

In most ornithopods the tail droops immediately behind the hips (Gilmore 1909; Galton 1970). In iguanodonts and hadrosaurs the tail base is arched up just a little. In most small ornithopods the end of the tail is stiffened by ossified rods; in iguanodonts and hadrosaurs almost the entire postcervical column is greatly stiffened by ossified rods

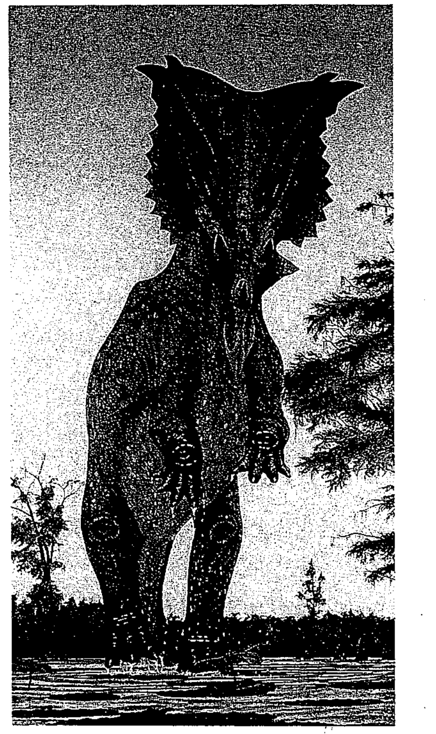


Figure 22. "Rearing *Chasmosaurus ?belli*." Rearing may have been an intimidating threat posture of ceratopsids; the object of this animal's attentions may be another member of the species or a predator. The rich skin topography is restored after skin impressions. Locale is a bald cypress lake with water lily and duckweed type plants in the Judith River Formation; the moon is about to occult Venus.

OPPOSITE
Figure 21. "Charging *Triceratops horridus* group." Even the biggest of the ceratopsians were built for rhinolike galloping. Fore-limb action is shown a little too erect (see Fig. 23b). Locale is a dried-out bald cypress swamp in the Lance-Hell Creek Formation. This painting has been substantially revised (for original version see Gould [1978, 1980]). Checklist 70.

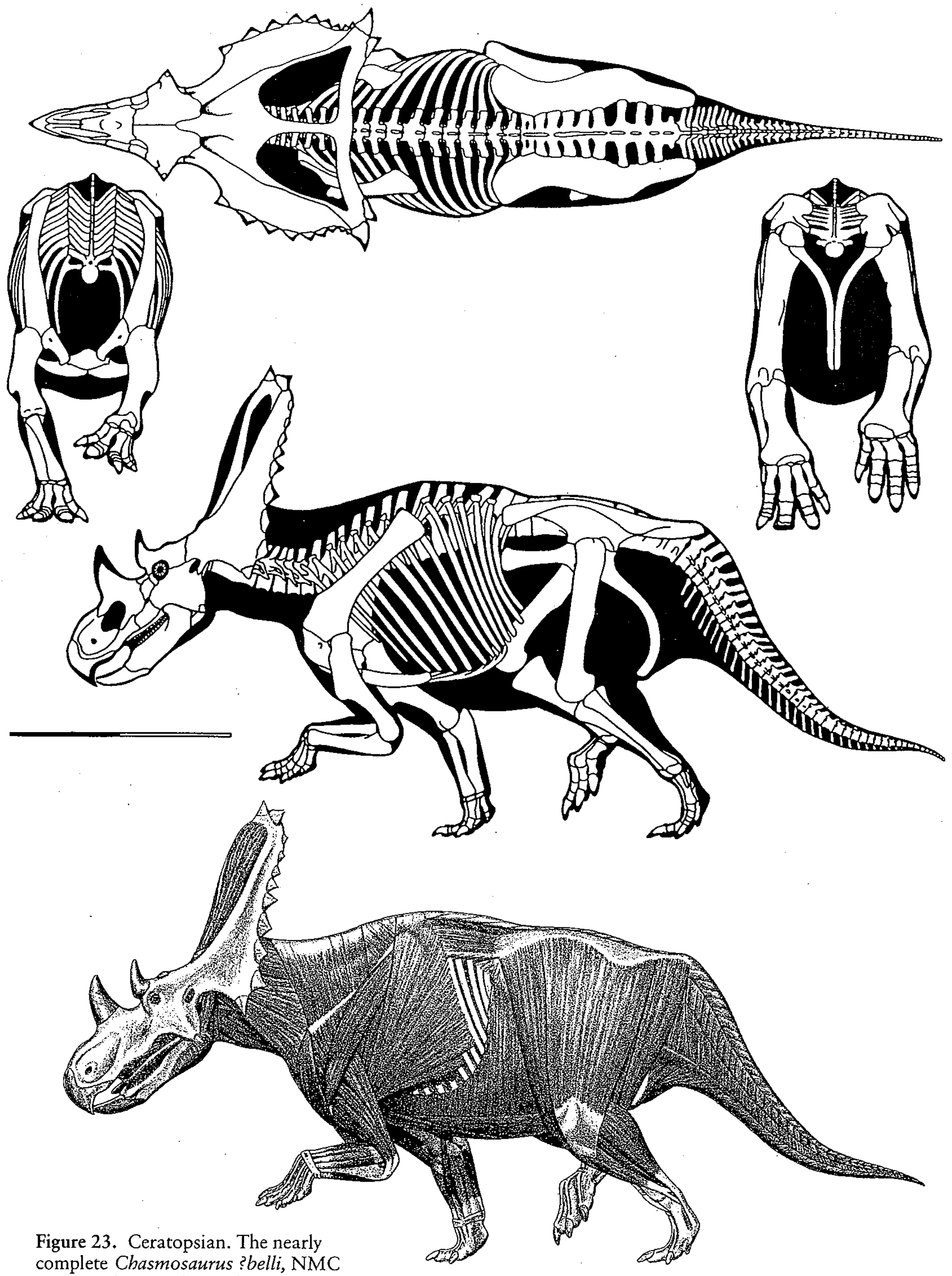


Figure 23. Ceratopsian. The nearly complete *Chasmosaurus ?belli,* NMC 2280, with some details from NMC 2245; data in part from Sternberg (1927) and new PANS mount by Carpenter. Scale bar equals 1 meter. Note the withers formed by the tall shoulder spines and the impossibility of the dorsal neck muscles attaching to the top of the frill.

and restrictive articulations. Although all ornithopods could rear (Maryanska and Osmolska 1984) to high browse, display, or in the case of camptosaurs and iguanodonts fight, the many restorations that show iguanodonts and hadrosaurs resting kangaroo-style on bent tails are incorrect.

In most small ornithopods and camptosaurs the fore limbs are too short to use at any but the slowest speeds. In *Tenontosaurus, Muttaburrasaurus,* iguanodonts, and hadrosaurs the fore limbs are long-running organs, and trackways prove that the fore limbs were used at least occasionally (Norman 1980; Currie 1983). The common trackways showing only hind prints do not prove that they were walking bipedally because the hind feet may have wiped out the fore prints. The fastest gait of this long-fore-limbed species was probably a trot as the fore limbs are too slender to support a gallop. In most preiguanodonts the five fingers are free and bear hooves on the inner three. The four long toes are also free and underlain by small individual pads. Trackways and a recently discovered mummified hand (Currie personal communication) show that the iguanodont's and hadrosaur's three central fingers and hooves are encased in a single hooflike sheath. This is not a web as often thought, nor is digit II in a separate lobe as suggested by the damaged SM R.4306 (contra Bakker this book). The thumb is a great spike weapon in *Camptosaurus, Muttaburrasaurus* (Molnar 1982), and primitive iguanodonts; it dwindles in advanced iguanodonts and is lost in hadrosaurs. The outer digit is free and unhooved. As for the hind feet, trackways and mummies show the three short toes each underlain by a single diamond-shaped pad, backed by a fairly large central pad. The pigeon-toeing seen in ornithopod trackways is not due to bipedal waddling because it persists when the fore prints are present.

Small mosaic scales are known on hadrosaurs, iguanodonts, and tenontosaurs. The hadrosaur "mummies" are both extraordinary and underappreciated for the nearly complete information they provide on surface topography. They invariably show a frill running along most if not all the vertebral column. The frills are continuous skin ribbons in *Edmontosaurus* (Osborn 1912; Horner 1984) and *Hypacrosaurus* (Fig. 25; B. Brown 1916) or made of individual hornlets as in *Kritosaurus* (Parks 1920). The *Edmontosaurus* frill has rectangular dorsal serrations. The *Hypacrosaurus* frill is very deep over the neck and attaches to the crest, as it may have done in all crested hadrosaurs. Small, nonbony hornlets are found on the flanks or belly of some hadrosaurs (B. Brown 1916; Parks 1920). Vertical wrinkles mark some of the ribbon frills and other areas of the body. Most prominent of these are the large vertical skin folds enwrapping the neck base, shoulder, and upper arm. These are not artifacts caused by dessication because they are always present, always vertical, and never found elsewhere on the body. Yet most restorations ignore the dorsal frills, and almost all ignore the shoulder folds.

Some duckbills were giants of twelve to twenty or more metric tons (*Shantungosaurus,* Mesaverde tracks). Only sauropods were bigger.

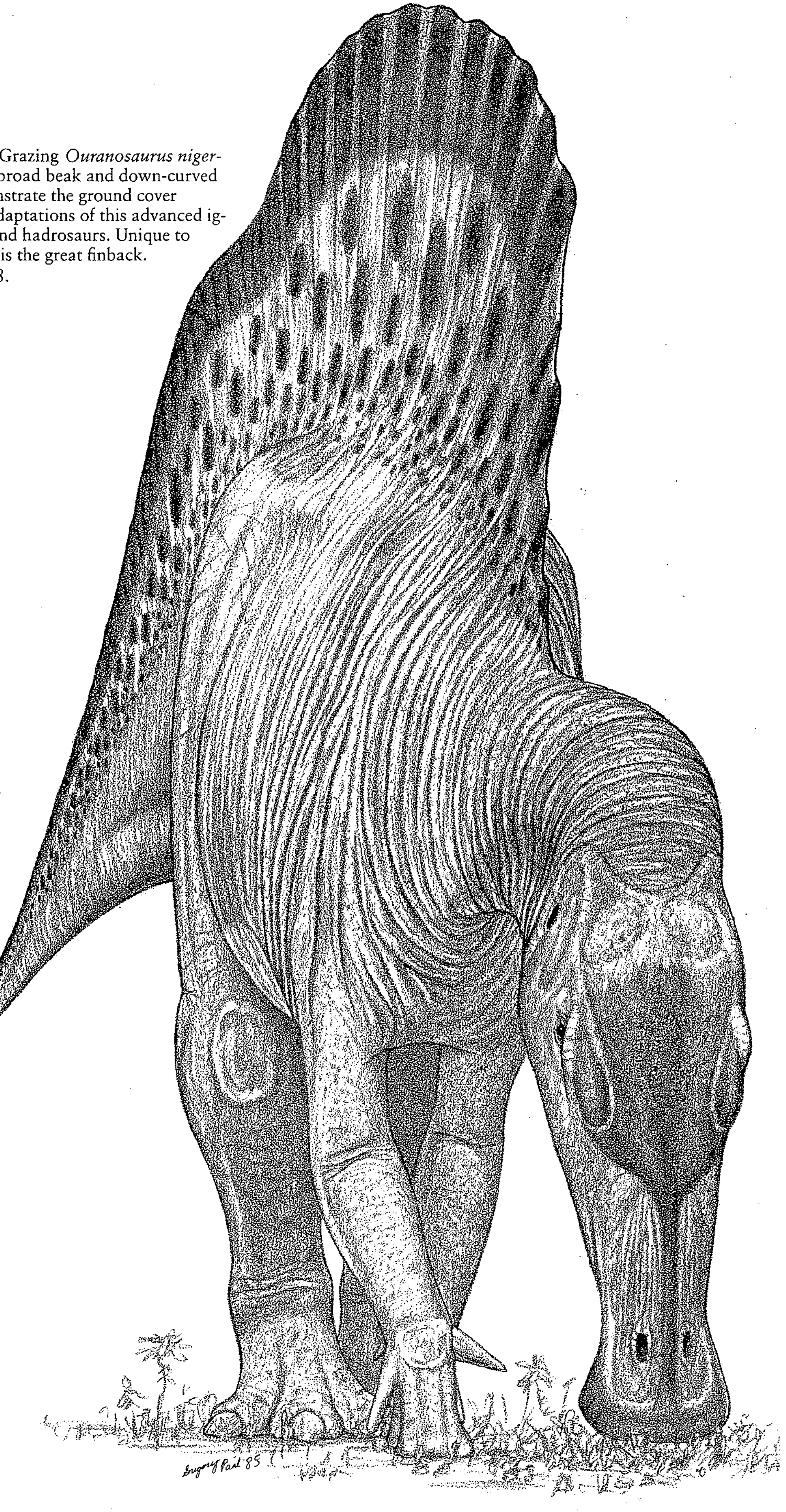
Virtually complete mummies make *Edmontosaurus annectens* and *Hypacrosaurus casuarius* the two most restorable published dinosaurs. The life restoration of the latter in Figure 25 is estimated to be eighty-five to ninety percent accurate.

The Science of Paleorestoration

Some paleontologists continue to consider paleorestoration as inherently unimportant and impractical. Actually we can no more observe how a living dinosaur population evolves than we can see their appearance. But as astronomers sample stars through their spectra, we can use indirect means to obtain information regarding the appearance of dinosaurs. In some cases dinosaurs can be restored with remarkably high fidelity, almost as accurately as some recently extinct animals. As for the importance of paleorestoration, it is just as interesting to know what a dinosaur looked like as it is to know its relationships. Proper restoration of the design of animals can be important toward understanding their function and ecology.

This paper is intended to reduce the frustrating number of mistakes plaguing the field. These errors cannot all be attributed to a lack of knowledge. Correct information has often been available for decades—the famous, yet underused *Edmontosaurus* mummy was published before

Figure 24. Grazing *Ouranosaurus nigeriensis*. The broad beak and down-curved back demonstrate the ground cover browsing adaptations of this advanced iguanodont and hadrosaurs. Unique to this species is the great finback. Checklist 78.



World War I. In part the problem stems from the postdepression doldrums that long afflicted dinosaurology. The field has revived since the mid-1960s, and dinosaur restoration has not only benefited from but contributed to this revival. Yet the skepticism and the noncritical attitude of some scientists, exhibits personnel, and editors hold it back.

Part of the solution is a more rigorous, critical attitude. The common assertion that there is always more than one way to restore a given animal is not true. Another problem is lavishly detailed restorations that do not capture the basic shape and form of the subject. It is more important to execute the distinctive profile of each dinosaur than to meticulously add hypothetical details. A different problem arises when fine wildlife artists produce cartoonlike renderings (notable exceptions are Kish's work [Russell 1977] and Bill Berry's Dinosaur National Monument restorations [White 1967]). More critical guidance is needed. Further, there must be solid reasons for alternative representations. Herbivorous dinosaurs should not be restored with hollow bellies when this violates all that is known about herbivore alimentary tracts. Hadrosaurs should always be restored with frills and vertical shoulder folds. And tails are best put where they belong, in the air.

Indeed, arching the sauropod's tails over the visitor's head brings us to another point. We need to be daring and bold. Not only are traditional concepts of dinosaur appearance no more intrinsically valid than controversial ones, more often than not they are incorrect. The reasons for illustrating alternative views of dinosaurs are excellent if not imperative.

THE ART

As well as being scientific, the best dinosaur restorations should also be artistic. Most dinosaur restorations are illustrations and do not possess that indefinable air that qualifies them as art. In this regard I disagree with photographic-image restorations. Extinct animals cannot be restored with complete confidence or be photographed. Art is the use of visual cues and creative license to convince people that they are seeing a version of reality.

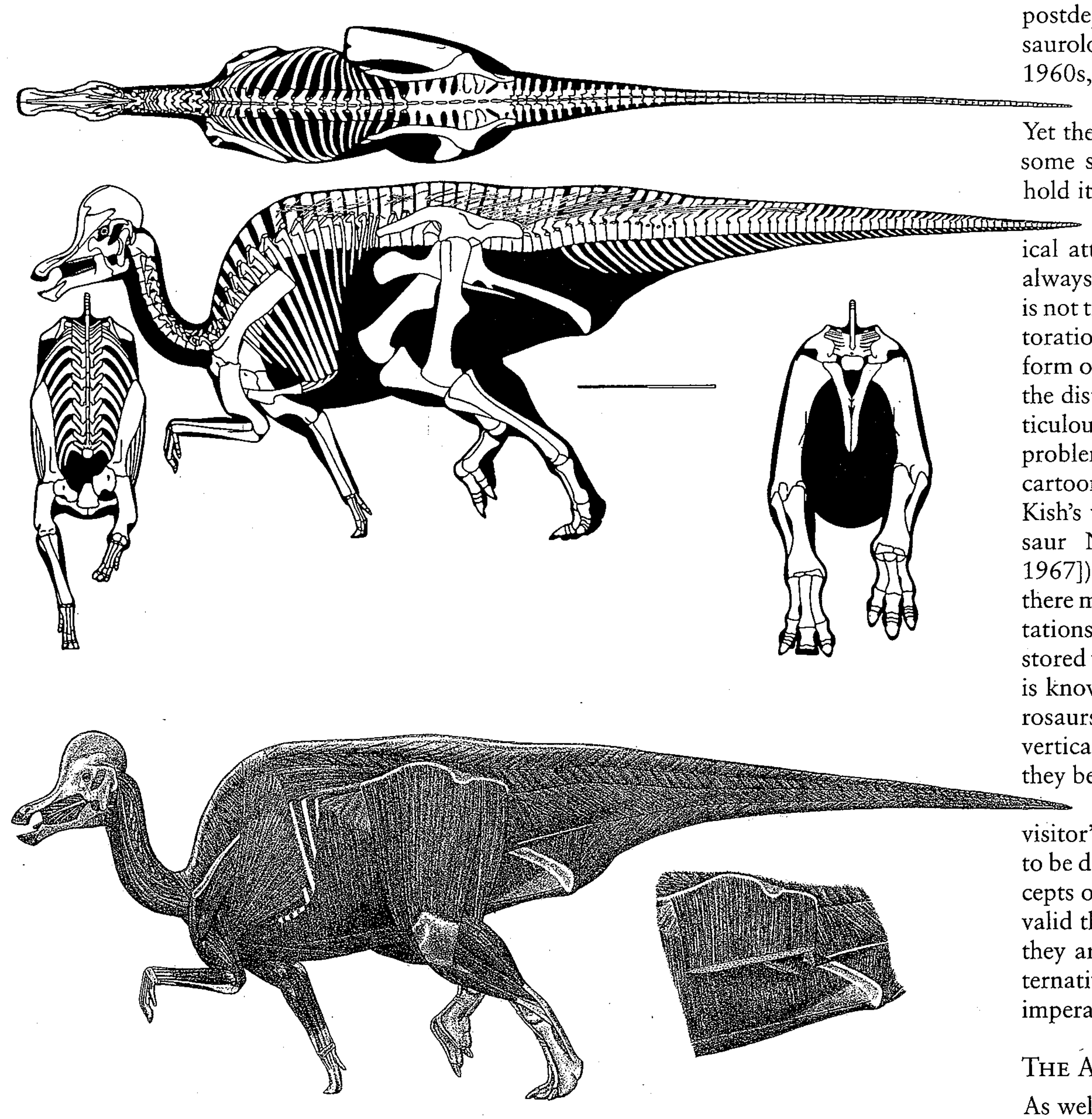


Figure 25. The duck-billed *Hypacrosaurus (= Corythosaurus) casuarius* holotype, AMNH 5240, a nearly complete male mummy in which much of the shown skin topography is preserved. Scale bar equals 1 meter; insert exposes the hip musculature. Fore limb after AMNH 5338; data from B. Brown (1916).

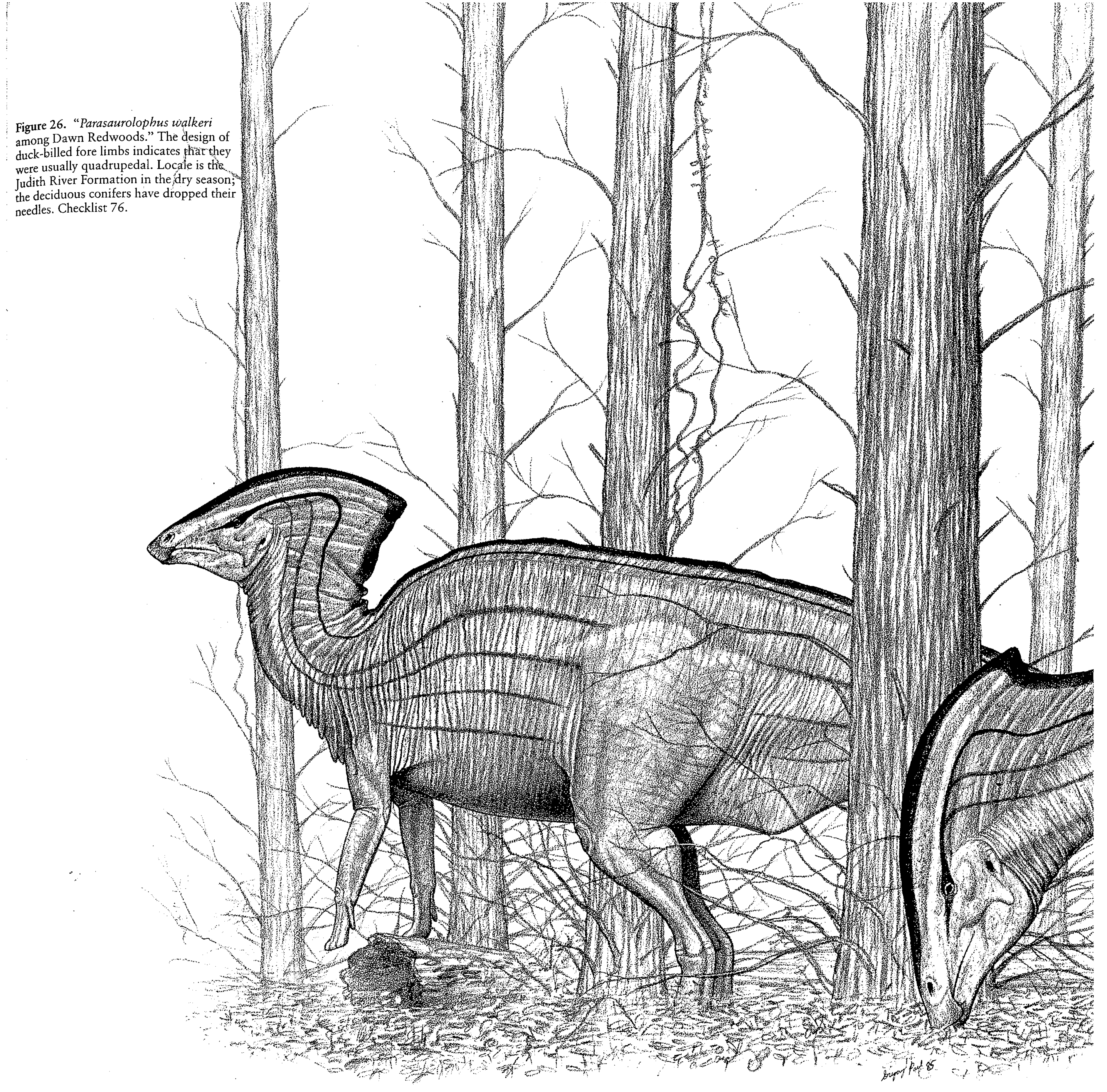


Figure 26. "*Parasaurolophus walkeri* among Dawn Redwoods." The design of duck-billed fore limbs indicates that they were usually quadrupedal. Locale is the Judith River Formation in the dry season; the deciduous conifers have dropped their needles. Checklist 76.

Paintings and other restorations should be just what they are, aesthetic and realistic illusions of how the subjects may have appeared in life. This brings us back to boldness, the importance of combining color, lighting, composition, and action to create a work that may even verge on the surrealistic but that is based on facts and possibilities. Such works not only inform, they challenge the viewer.

An important inspiration for me is the wildlife art of Shepard (1969). Indeed the composition of "*Brachiosaurus brancai* herd" (Fig. 7), my first professional and favorite restoration, is derived from one of his elephant scenes. The western equid scenes of Remington (1895) are another influence; "Charging *Triceratops horridus* group" (Fig. 21) especially owes much to his scenes of galloping horses.

Time constraints often prevent us from achieving what we would like, and balky exhibits departments and editors sometimes (but not always) get in the way. Often things just don't work out. But whenever possible the aim should be to render dinosaurs as rigorous, scientific, yet provocative and dynamic pieces of art.

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