Skeletal reconstruction and life restoration of *Sauropelta* (Ankylosauria: Nodosauridae) from the Cretaceous of North America

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A skeletal reconstruction and life restoration are presented for the Early Cretaceous nodosaurid ankylosaur *Sauropelta edwardsi*. This composite is based on several partial skeletons having armor preserved *in situ* from the Lower Cretaceous Cloverly Formation of Wyoming and Montana. Comparison of foot morphology with that of the ichnofossil *Tetrapodosaurus borealis*, from the Lower Cretaceous Gething Formation of British Columbia, suggests that the footprint is that of *Sauropelta*. A hypothesis is presented suggesting that most ankylosaurs are found on their backs because of bloating.

Une reconstruction du squelette et une restitution des conditions de vie sont présentées pour l'ankylosaurien nodosauride *Sauropelta edwardsi* du Crétacé inférieur. Cette reconstruction composite et la restitution sont fondées sur plusieurs pièces de squelettes équipés d'une armature préservée *in situ* dans la formation de Cloverly du Crétacé inférieur du Wyoming et du Montana. Une comparaison de la forme des pieds avec l'ichnofossile *Tetrapodosaurus borealis* de la formation de Gething du Crétacé inférieur de la Colombie-Britannique révèle que l'empreinte du pied est celle de *Sauropelta*. Une hypothèse est présentée suggérant que les ankylosauriens qui sont trouvés le sont à cause du boursouflement du dos.

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Introduction

Nodosaurid ankylosaurs were among the earliest dinosaurs described, with *Hylaeosaurus armatus* named by Mantell (1832) just seven years after *Iguanodon*. *Hylaeosaurus* also has the distinction of being the first dinosaur for which a life restoration was attempted. This was a life-size model constructed at Crystal Park by Hawkins in 1854 (see Colbert 1968, Pl. 6, central spined figure misidentified as *Megalosaurus* in the caption). Today the restoration is known to be mostly the imagination of Sir Richard Owen and Hawkins. A more recent life restoration by Olshevsky (1979) is based on the articulated neck and tail with some armor *in situ* figured by Owen (1858, Pl. 4, 10). However, the number and shapes of the lateral cervical spines in Olshevsky's restoration do not match the figured specimen. Furthermore, Olshevsky has added stegosaurlike plates along the midline of the tail, which do not appear in the tail figured by Owen but seem to be adapted from Nopcsa's (1905) reconstruction of *Polacanthus*.

Not until 1905 was an attempt made of a skeletal reconstruction for a nodosaurid: Nopcsa (1905) presented a skeletal and dermal armor reconstruction of *Polacanthus foxii* Hulke 1881 based on the type. Because the skeleton was incomplete Nopcsa modeled the missing parts after the better known *Stegosaurus* and *Scelidosaurus* to which he thought *Polacanthus* was related. However, because little of the material was found articulated, Nopcsa had little basis for his reconstruction.

A life restoration of *Polacanthus* has been attempted by Neave Parker (Colbert 1961, Pl. 76). Parker's restoration is based on Nopcsa's (1905) skeletal reconstruction and thus reflects his biases. Furthermore, Parker gave her restoration a *Stegosaurus*-like head, reflecting the once held belief that ankylosaurs were related to stegosaurs.

The only other nodosaurid for which a skeletal reconstruction has been attempted was presented by Lull (1921) for the type of *Nodosaurus textilis*. Because of the incompleteness of the material, Lull utilized Brown's (1908) reconstruction of *Ankylosaurus* for information on the presacral vertebrae, ribs, and scapula. The skull is a compromise between the skulls of *Scelidosaurus* and *Ankylosaurus*, but the result does not look nodosaurid. The reconstruction looks more plausible than Nopcsa's (1905), but fails to show the anterior ribs curving posteriorly, lacks a mammalianlike acromion process on the scapula, lacks a prominent deltopectoral crest on the humerus, does not have a ventrally projecting ischium, and does not show chevrons anteroposteriorly elongated.

Lull (1921) did not attempt a life restoration beyond a simple body outline. However, Olshevsky (1979), Halstead and Halstead (1981), and Stout (see Glut 1982) have made restorations, and their results differ considerably. Olshevsky relied on the undemonstrated synonymies of Coombs (1978a) whereby *Stegopelta* and *Heirosaurus colei* are assigned to *Nodosaurus*. Considering the fact that there is no overlap in armor type between *Stegopelta* and *H. colei* on the one hand, and *N. textilis* on the other, this synonymy is untenable. Thus, Olshevsky's restoration shows a greater diversity in armor type than probably existed on *Nodosaurus*.

The life restoration of Halstead and Halstead (1981) is similar to the body outline by Lull (1921). The neck, back, and tail are shown encased in transverse bands of nodular rectangular plates alternating with bands of rectangular flat plates. This type of armor was figured by Lull (1921, Pl. 1, figs. 1, 3) from near the pelvis. Considering the diversity of armor in the neck–shoulder region of nodosaurids in armor preserved *in situ*, it is doubtful that *Nodosaurus* was uniformly covered in only two types of armor. Unfortunately, this cannot be verified until another, more complete specimen is recovered.

Stout (see Glut 1982), on the other hand, has scattered short spines on the neck and back despite the absence of such spines on the preserved section of armor in *Nodosaurus*. As with Olshevsky (1979), Stout may have been influenced by the synonymies of Coombs.

Besides *Hylaeosaurus* and *Nodosaurus*, numerous other nodosaurid life restorations have been attempted. Many of these conflict with one another and often have little factual basis. Most notable among these are the restorations of *Acanthopholis* (Glut 1982, p.38), *Edmontonia* (Glut 1972, p. 22), *Palaeoscincus* (Matthew 1922, pp. 339, 342; Olshevsky 1979; Halstead and Halstead 1981, Fig. 95; Czerkas and Glut 1982, Fig. 104), *Silvasaurus* (Eaton 1960, Fig. 21; Olshevsky 1979; Halstead and Halstead 1981, Fig. 91; Stout 1981, p. 131), and
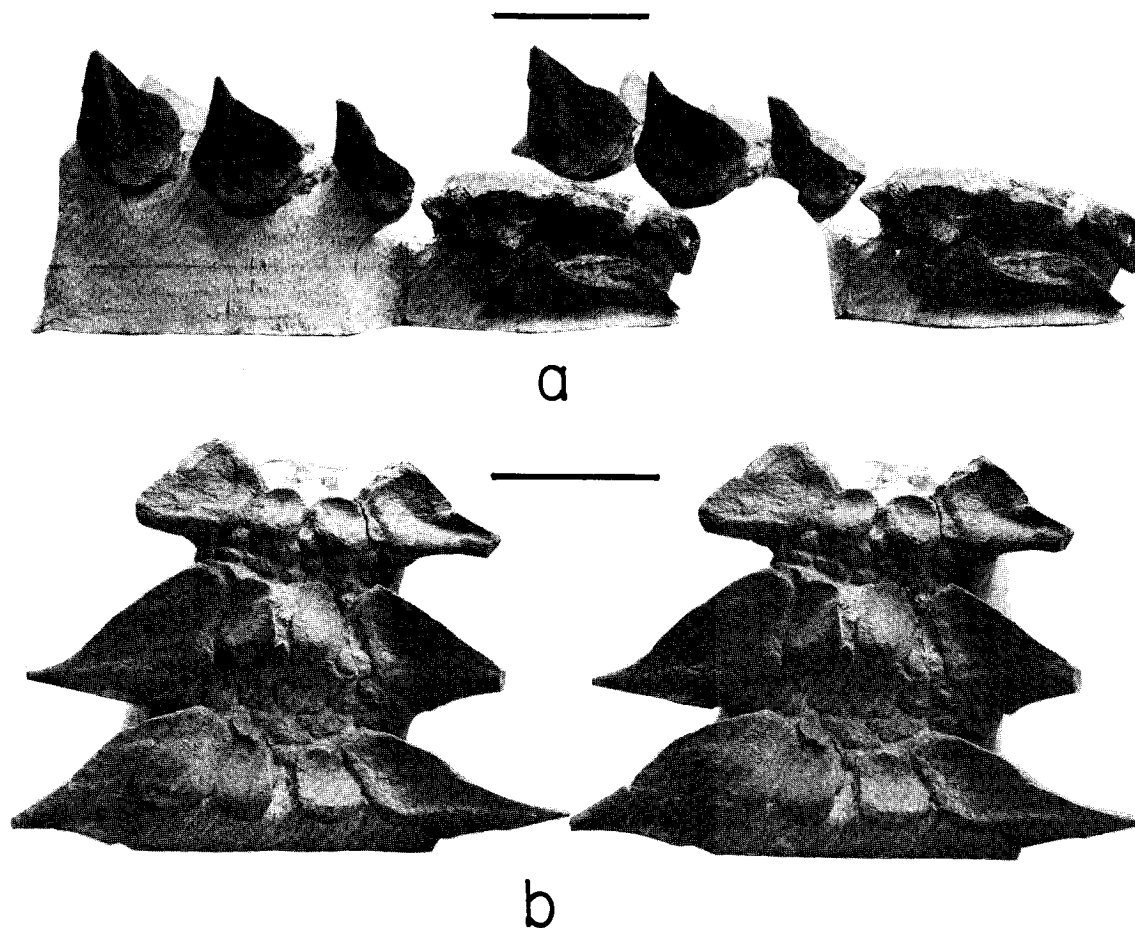
FIG. 1. *Sauropelta edwardsi* (AMNH 3035). (*a*) Stereophotograph of cervical armor and skull in lateral view. (*b*) Stereophotograph of the cervical armor in dorsal view. Heavy bars = 25 cm.

Struthiosaurus (Nopcsa 1929, Pl. 6; Glut 1972, p. 186, 1982, p. 232; Halstead and Halstead 1981, Fig. 89; Stout 1981, p. 131; Lambert 1983, p. 183). Part of the problem is due to the artist's restoration not reflecting the fossil material (e.g., note differences between the cervical plates and spines in Knight's restoration of *Palaeoscincus* in Czerkas and Glut (1982, Fig. 104) and the actual specimen in Matthew (1922, pp. 334, 335)). The problem is made worse when paleontologists treat the life restorations based on fragmentary material as fact rather than speculation (e.g., Halstead and Halstead 1982, p. 152 on *Acanthopholis horridus*).

Because of flaws in all previous nodosaurid restorations, a skeletal reconstruction and life restoration have been prepared for the Early Cretaceous *Sauropelta edwardsi*. These are based on articulated specimens retaining armor *in situ*.

Sauropelta

Sauropelta edwardsi was named by Ostrom (1970) for material collected from the Lower Cretaceous Cloverly Formation of Wyoming and Montana. This material was collected by the American Museum of Natural History (AMNH) during the 1930's and by the Yale Peabody Museum (YPM) during the 1960's. Several partial skeletons are included among the material, two of which retain a considerable amount of armor preserved *in situ*. These two specimens, AMNH 3035 and AMNH 3036, form the basis of the skeletal reconstruction and life restoration. This was supplemented by other material in the AMNH and YPM collections, including the type specimen

AMNH 3032. The osteology of *Sauropelta* has been discussed by Ostrom (1970), with additional comments by Coombs (1978 *a-c*, 1979).

AMNH 3036 is the single most complete nodosaurid specimen from North America and was previously figured dorsally (Colbert 1961, Pl. 75) and ventrally (Anonymous 1937, p. 32). The specimen lacks the skull, neck, and anteriormost dorsals (plus their associated armor), distal portion of the tail, left forelimb (including scapula and coracoid), some of the right manus phalanges, and lower parts of the left hind limb. An unpublished manuscript by Brown (1933) states that the specimen was found on its back with the front of the body and tail eroding out. Skull fragments nearby suggest that the specimen was complete when buried. However, these fragments have not been located in the AMNH collections, so their identification cannot be verified.

AMNH 3035 is not as complete as AMNH 3036, but retains the cervical armor and a portion of the skull *in situ* (Fig. 1). A brief description of the skull was given by Ostrom (1970), with additional comments by Coombs (1971). A detailed description of the skull is currently in preparation by Coombs (personal communication, 1982).

AMNH 3036 forms the basis for the skeletal reconstruction, with missing parts scaled from AMNH 3032 (the type) and AMNH 3035. Measurements for AMNH 3036 are presented in Table 1, and those of other specimens are given by Ostrom (1970, Table 5). As reconstructed (Figs. 2, 3) AMNH 3036 was about 5.2 m long with an estimated live body weight of about 1500 kg (based on a clay model; see Colbert (1962) for

TABLE 1. Measurements of *Sauropelta edwardsi*, AMNH 3036

		Length (cm)	Width (cm)
Presynsacral centrum	10	8.1	
	9	7.9	
	8	7.8	
	7	8.8	
	6	9.1	
	5	8.7	
	4	8.8	
	3	9	
	2	8.4	
	1	8	
Synsacrum		72.8	
Synsacrum anterior face			5.2
Caudal centrum	1	7	10.6
Across transverse processes			40.8
	2	6.9	10.7
Across transverse processes			37.8
	3	5.9	11
Across transverse processes			34.4
	4	6.1	9.8
Across transverse processes			29.5
	5	5.6	9.2
Across transverse processes			—
	6	6	9
Across transverse processes			23.7
	7	6.3	8.9
Across transverse processes			22.5
	8	Obscured	
	9	Obscured	
	10	Incomplete	
	11	7	
	12	7	
	13	6.7	
	14	7.1	
	15	6.8	
	16	6.7	
	17	7	
	18	Obscured	
	19	Obscured	
	20	Obscured	
	21	7.4	
	22	6.6	
	23	6.8	
	24	7	
	25	Crushed	
	26	6.3	
	27	Crushed	
	28	Crushed	
	29	6.9	
	30–40	Reconstructed	
Scapula (right)		48.5	
Coracoid (right)		13.3	20.5
Humerus (right)		49.5	
Ulna (right)		48.5	
Radius (right)		32.5	
Metacarpal	I (right)	7.4	
	II	9.2	
	III	11.3	
	IV	11.8	
	V	10.2	
Phalanges	I-1	—	
	I-2	—	
	II-1	2.6	
	II-2	—	
	II-3	—	

TABLE 1. (*Concluded*)

|		Length (cm)	Width (cm)
	III-1	2.8	
	III-2	1.6	
	III-3	.8	
	III-4	5.0	
	IV-1	2.4	
	IV-2	1.3	
	IV-3	6.1	
	V-1	4.5	
	V-2	—	
Ilium (left)		96.5	
Across sacrum			129.5
Pubis		Incomplete	
Ischium		49.5+	
Femur (left)		70	
Femur (right)		53.5	
Fibula (right)		53.5	
Metatarsals (arrangement uncertain)	A (right?)	9.4	
	B	12.0	
	C	9.3	
Phalanges (right?)	B-1	12	
	D-2?	4.8	
	D-3?	7.5	

details of the technique).

Sauropelta probably has eight cervical vertebrae, 16 dorsals (the last four of which are fused into a presacral rod), and at least 40 caudals. AMNH 3036 has 29 caudals preserved, and Ostrom (1970) reported at least 39 present in AMNH 3032. In both specimens an unknown number of caudals are missing. Forty caudals is therefore a conservative estimate, with the actual count possibly exceeding 50. This high number produces a remarkably long tail, almost half the total length of the animal. Ossified tendons are present starting at least at the seventh dorsal and continuing to the end of the tail.

As with ankylosaurids and other quadrupedal ornithischians, the neck of *Sauropelta* is short, the scapula and limbs are massive, the pelvis is enlarged, the forelimbs are shorter than the hind, causing the back to be arched, and the feet are short and broad. All of these features appear to be adaptations for a very heavy animal.

The reconstruction of the dermal armor pattern is based on AMNH 3035 and AMNH 3036, supplemented by AMNH 3032. Ostrom (1970) briefly discussed the armor, as did Coombs (1971). Neither, however, has discussed the arrangement of the armor in any detail.

The cervical armor consists dorsally of oval plates that are slightly scooped anterodorsally and rise to a low dome posteriorly (Fig. 1b). These plates are flanked laterally by triangular spines projecting lateroposteriorly (Fig. 1 a and b). These spines have a sharp keel along the anterior edge and are set at an angle so that the edge of the keel faces anterodorsally. The spines increase in size posteriorly on the neck and reach their largest size on the anteriormost part of the body (Fig. 3). It should be mentioned that Ostrom (1970) suggested that *Sauropelta* may have had a spike tail similar to *Stegosaurus*, based on a fragmentary large spine. Recently, however, W. Coombs located the missing base to this spine (Fig. 4a), which permits a reassessment of Ostrom's suggestion. Comparison with the caudal spine of *Stegosaurus* (Fig. 4) reveals the following differences: the anterior edge is keeled near the base and the
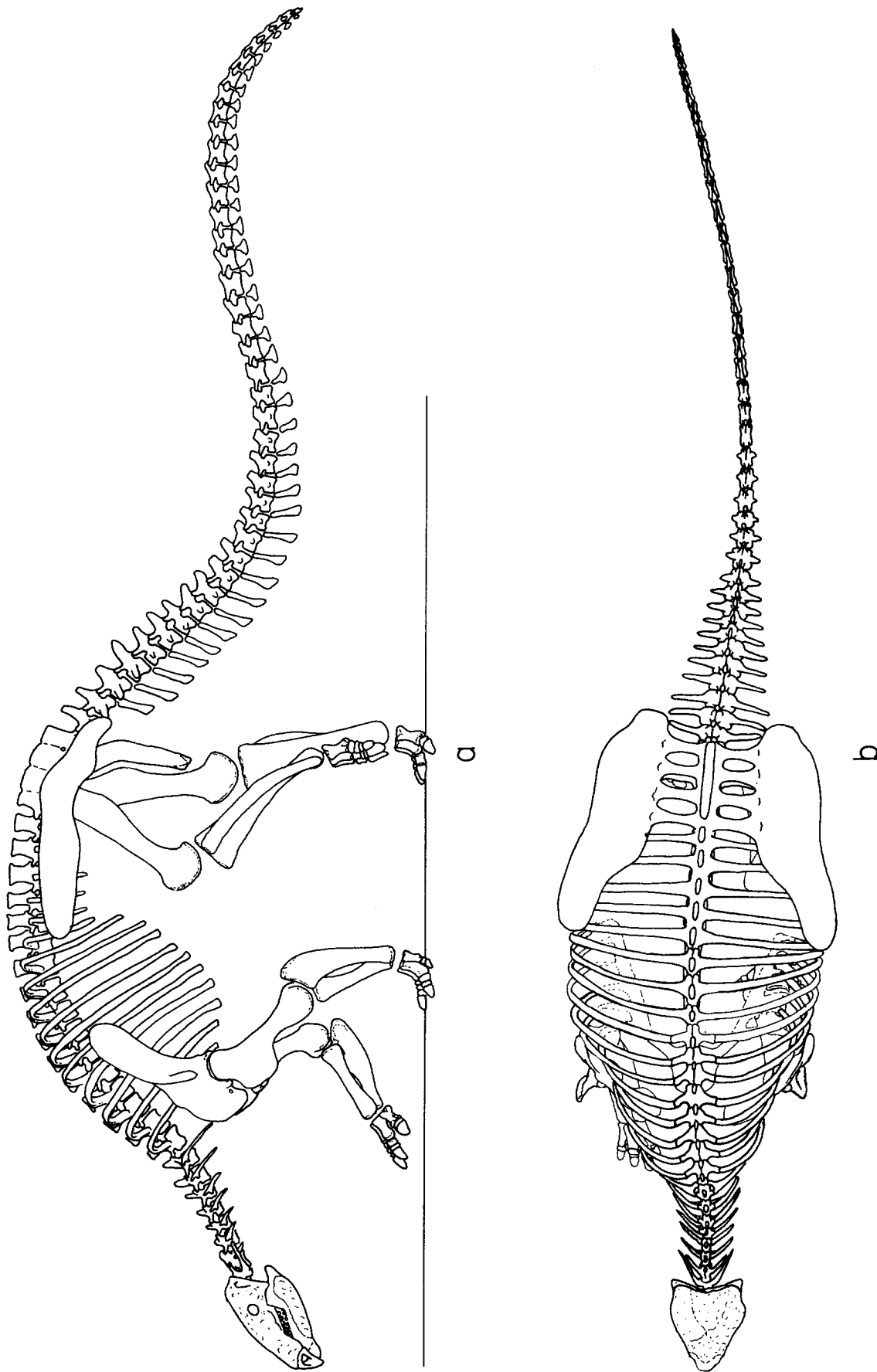
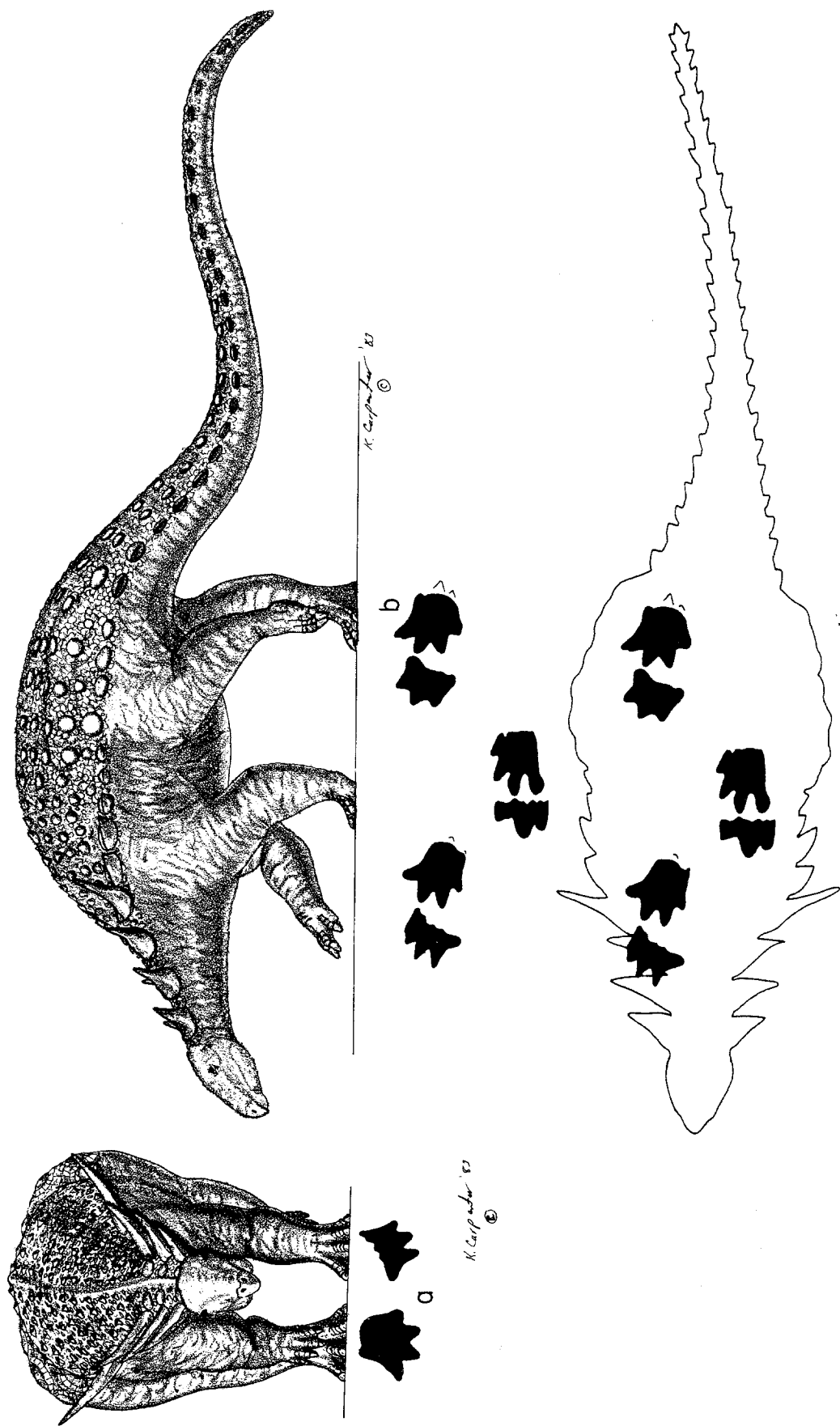FIG. 2. Skeletal reconstruction of *Sauropelta edwardsi*. (*a*) Lateral view. (*b*) Dorsal view.

FIG. 3. Life restoration of *Sauropelta edwardsi*. (*a*) Front view showing medially placed feet. (*b*) Side view. (*c*) Top view. Black footprints below (*b*) are those of *Tetrapodosaurus borealis* as interpreted by Sternberg (1932).

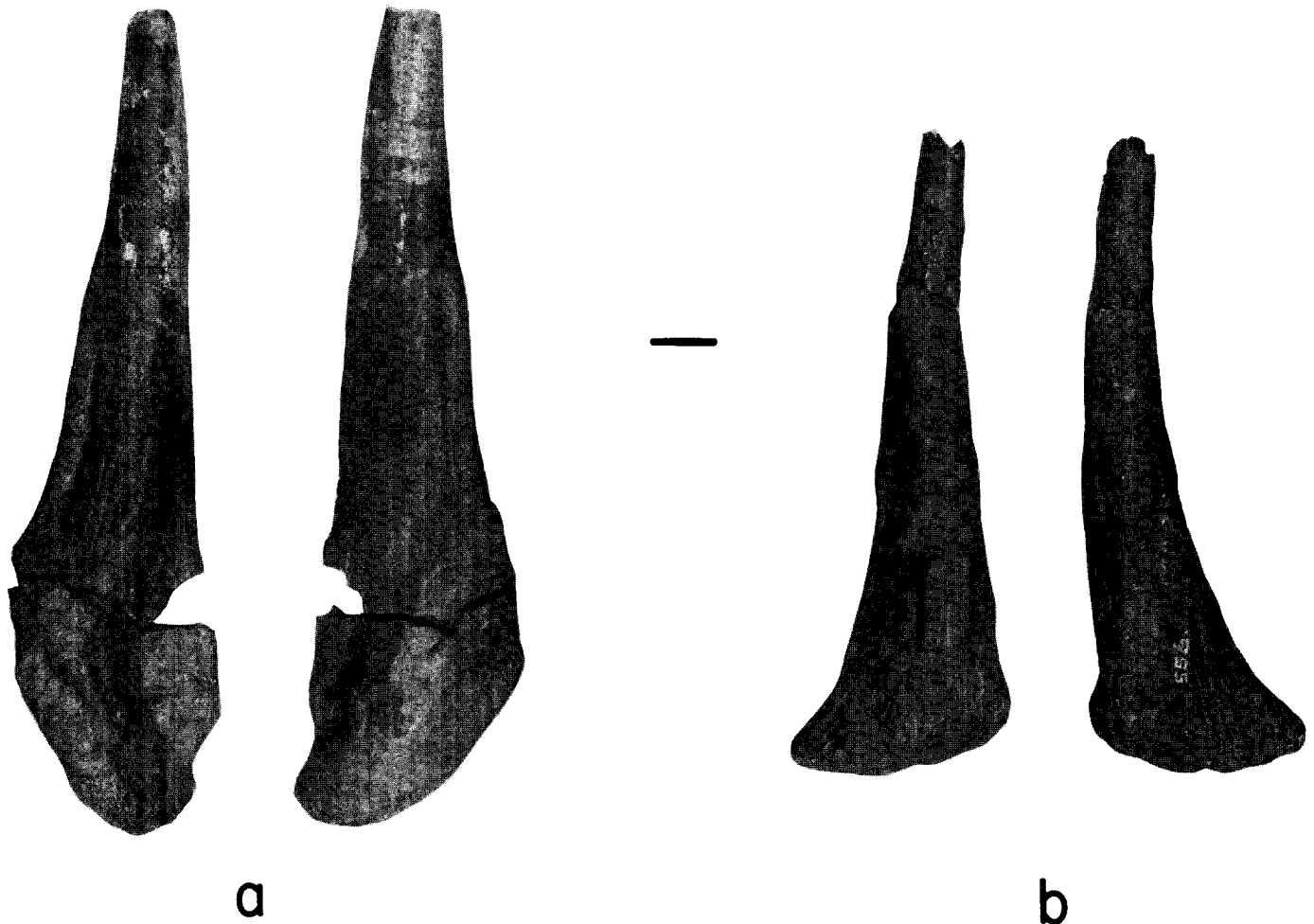FIG. 4. Comparison of the large shoulder spine of *Sauropelta* with a tail spine of *Stegosaurus*. (*a*) *Sauropelta edwardsi*, AMNH 3032. (*b*) *Stegosaurus* sp., AMNH 556.

base is strongly beveled. Both of these features characterize the cervical spines shown in Fig. 1.

The rest of the lateral armor of the body and tail consists of hollow, dorsoventrally compressed, triangular plates. On the body these plates decrease in height posteriorly, and those across the thighs have only low keels. On the tail, the first plate is the tallest and successive plates decrease in height posteriorly.

Dorsally, the body is covered by very low cones arranged in transverse rows. The cones are separated by irregular ossicles that floated in the skin and permitted lateral movements of the body. The sacral armor consists of large, circular, slightly domed plates set in transverse rows and separated by an interlocking mosaic of irregular scutes. The presacral rod, anteriorly expanded ilium, and tightly interlocking armor prevented any movement in this region. Doming of these plates reaches its maximum on the sides of the body. The circular plates continue onto the dorsal surface of the tail and are separated by irregular ossicles.

As restored (Fig. 3) *Sauropelta* is a large, very broad animal. Heavy weight-bearing adaptations include the short broad feet and robust limbs, which were placed beneath the body near the midline (Figs. 3*a*, 5*a*). Anatomical reasons have been given to explain why the limbs of quadrupedal ornithischians (including ankylosaurs) had to have been positioned beneath the body and not sprawled (Carpenter 1982). I have also suggested that the

footprints *Tetrapodosaurus borealis* from the Lower Cretaceous Gething Formation of British Columbia are not those of a ceratopsian, as Sternberg (1932) suggested, but are those of a nodosaurid. This hypothesis is strengthened by the structure of the feet in *Sauropelta*. As can be seen in Fig. 5*b*, the digit count of five on the manus and four on the pes is exactly the same as for *Tetrapodosaurus*. Because the Gething Formation is the same age as the Cloverly Formation (Ostrom 1970; Stott 1975), and because the feet of *Sauropelta* match *Tetrapodosaurus* well, *Sauropelta* probably is the footprint maker.

Figure 5*b* suggests the manus and pes were encased in heavy skin, with a "web" of skin between the toes. The toes are spread out, distributing the weight over a large area. Although a new interpretation of the *Tetrapodosaurus* footprints by P. Currie (personal communications, 1983) may modify the exact shape of the heel area, the hind foot clearly shows an elephantine pad that would cushion the step. Similar pads have been noted in sauropod footprints (Lockley *et al.*, in preparation).

Comments on preservation

Sternberg (1970) observed that most ankylosaur specimens from North America are preserved upside down; he suggested this was because the heavy armor caused the dead animals to float on their backs until they sank. Nopcsa (1928), on the other hand, believed that *Scolosaurus* (= *Euoplocephalus*) either rolled down a slope, coming to rest upside down where it
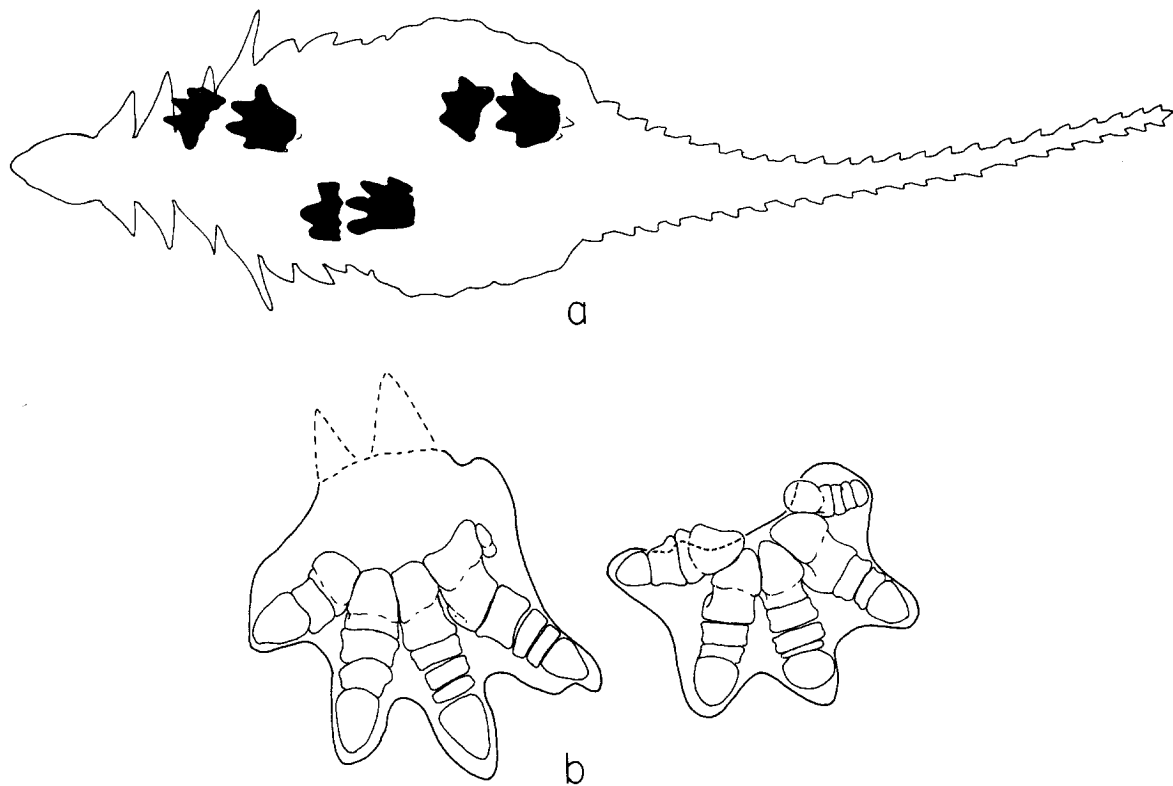
FIG. 5. (a) Body outline of *Sauropelta* superimposed over the footprints *Tetrapodosaurus* showing the narrowness of the gait. (b) Left manus (AMNH 3036) and right pes (AMNH 3032, reversed) of *Sauropelta* superimposed on the footprints *Tetrapodosaurus*.

perished, unable to right itself, or it was flipped over by a carnosaur.

These hypotheses have numerous flaws that make them questionable. Sternberg (1970), for example, erroneously assumed that dermal armor is extremely heavy in the living animal. Most armor plates, however, have a spongy core and a dense cortex. Fossilization fills the spongy core with minerals, thus exaggerating armor weight. The decomposition of elephant carcasses (Coe 1978) and cows (personal observations), suggests that bloating of the ankylosaur body and limbs would have caused the animal to float on its side until sinking. The weight of the limbs would prevent the body ankylosaur from rolling onto its back. But decomposition gases in the limbs would also prevent the weight of the limbs from rolling the bloated body right side up in the water. As for Nopcsa's (1928) suggestion that *Euoplocephalus* might have overturned like a turtle, the general flatness of the Late Cretaceous coastal plain would not provide many opportunities for that. Also, the body of *Euoplocephalus* (or any ankylosaur for that matter) is rotund enough (Carpenter 1982, Fig. 2c) that the animal would not have been trapped on its back. The rotund body also makes it unlikely that a carnosaur could flip a struggling 2000 kg ankylosaur onto its back like a helpless turtle.

Observations on road-killed armadillos (*Dasypus novemcinctus mexicanus*) in warm and humid Mississippi suggest another explanation of why ankylosaurs are found on their backs. Armadillos, if not squashed, are often knocked to the side of the road where they lie dead on their side. As decay progresses, the body and limbs bloat, with the limbs extending stiffly away from the midline. As the angle between the limbs increases because of bloating, the limbs on the lower side press against the ground, often causing the animal to roll onto its back. Soon after, maggots vent the body gas and limbs col-

lapse. Although the observations on road-killed armadillos were made on specimens exposed to the sun on a hard flat surface, the same processes were repeated for a fresh road kill (less than 6 h old) that was placed in a cypress swamp less than a metre from the water edge (along the Pearl River, Jackson, Mississippi). Similarly, a dead ankylosaur in a warm, humid environment, lying on its side, could eventually have rolled over because of its rotund (almost oval in cross section) body.

Objections might be raised about using a 7 kg armadillo to interpret the decomposition behavior of a 2000 kg ankylosaur, but decomposing elephants (Coe 1978) and cows (personal observations) exhibit many of the same stages as dead armadillos. They do not roll onto their backs because their bodies are laterally compressed. However, one cow has been observed in Wyoming almost on its back and it seems it would have been if the body had been broader.

Ankylosaurs from the Mongolian People's Republic differ from those of North America in that they are not always found on their backs (e.g., Kielan-Jarowowska 1975, Fig. 10). These, however, appear to have been buried in dunal deposits (Gradzinski and Jerzykiewicz 1974), which may have been from sandstorms. Support for this hypothesis is seen in several *Protoceratops* skeletons found in a kneeling position (G. Paul, personal communication, 1983) in the Gobi Desert. The fact that most North American ankylosaurs are preserved in channel deposits is to be expected if most of the articulated Late Cretaceous dinosaur specimens represent drought fatalities (Carpenter, in preparation).

Acknowledgments

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