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THE SEGNOSAURIAN DINOSAURS: RELICS OF THE PROSAUROPOD–ORNITHISCHIAN TRANSITION?

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ABSTRACT—*Segnosaurus* Perle, 1979, and *Erlikosaurus* Barsbold & Perle, 1980, are recently described dinosaurs of unusual form from the Late Cretaceous of Mongolia. Both taxa are medium-sized herbivores with small skulls, beaks, spatulate teeth, retroverted pubes, and broad four-digit hindfeet. Barsbold and Perle consider them to be theropods. However, the feet of segnosaurs are much less derived than are the bird-like feet of theropods. Further, the segnosaurs do not show any distinctive theropod-like characters that justify their assignment to this group. They appear, instead, to be derived prosauropods with a number of early ornithischian adaptations. Notable among these ornithischian-like adaptations are their beaked jaws with cheeks. A cladistic comparison of the segnosaurs with thecodonts and early dinosaurs of the Triassic suggests that, despite their late appearance, the segnosaurs are phylogenetic intermediates between herbivorous prosauropods and early ornithischians. As such the segnosaurs strengthen the hypothesis of dinosaur monophyly. Segnosaurs cannot be placed in the theropods, but traditional schemes of dinosaur classification do not recognize the possibility of dinosaur monophyly. Here the segnosaurs are considered to represent a clade between the prosauropods and ornithischians.

INTRODUCTION

Whether dinosaurs arose from one or from multiple thecodont ancestors is an important issue of dinosaur phylogeny (Bakker and Galton, 1974; Bakker, 1975; Bonaparte, 1975, 1976; Cooper, 1980; Charig, 1976; Cruickshank, 1979; Thulborn, 1980; Chatterjee, 1982). Data gathered by Bakker, Galton, Bonaparte, and Cooper suggest that the earliest herbivorous prosauropod dinosaurs and the earliest predatory theropod dinosaurs share a common ancestry among lagosuchid protodinosaurs. The herbivorous ornithischian dinosaurs are in turn derived directly from prosauropods. New support for the hypothesis of dinosaur monophyly has appeared from an unexpected quarter in the form of the segnosaurs, dinosaurs recently discovered in the Late Cretaceous of Mongolia. A cladistic analysis suggests that the segnosaurians, despite their late appearance, are derived prosauropods that show some ornithischian adaptations. In other words, they are late surviving relics of the Triassic prosauropod–ornithischian transition.

Two genera of segnosaurs have been described, *Segnosaurus* Perle, 1979, and *Erlikosaurus* Barsbold and Perle, 1980. Both are beaked, have small skulls and spatulate teeth, are opisthopubic, have broad, four-digit hindfeet, and both are medium-sized (Barsbold, 1979; Barsbold and Perle, 1979, 1980; Perle, 1981). Barsbold and Perle (1980) did not compare the segnosaurs to prosauropods or ornithischians. Rather they considered them to be aberrant members of the predatory dinosaur group Theropoda and erected for them a new infraorder, the Segnosauria. Romer (1966) defines the Theropoda as those dinosaurs that have blade-like teeth, bird-like hindfeet and are obligatory bipeds. This is an excellent minimal definition of the theropod clade. The evolution of the three-toed bird foot with a distally placed hallux is a major adaptation of theropods and birds. It is distinctive from all other tetrapod feet and may have evolved only once. Additionally, Romer's definition incorporates all the classic theropod genera from the Triassic *Coelophysis* to the Cretaceous *Tyrannosaurus*. But the spatulate-toothed, herbivorous, four-toed segnosaurians clearly fall outside of the boundaries of Romer's definition.

COMPARATIVE MORPHOLOGY

Pes—The hindfoot of segnosaurs is especially important. Barsbold and Perle (1980) suggest that "the distinctive characters of Segnosauria may be derived from the general theropod and saurischian pattern." But the pes of segnosaurians in particular contradicts this assertion, for deriving segnosaurians from theropods is possible only if a radical reversal in hindfoot morphology occurs. To become segnosaurian, the narrow, laterally compressed, functionally tridactyl hindfoot of theropods, with its reduced, distally placed, reversed hallux and splint metatarsal V, would have to revert to a more archaic, broad, functionally tetradactyl pattern (Fig. 1). In the latter, basal dinosaurian style pes—which is the kind found in segnosaurs—the large, unreversed first digit articulates with the ankle, and metatarsal V is short and stout. Such a reversion

is not impossible, but can conservatively be considered unlikely. In the massiveness of digit I and its claw weapon, and in overall proportions the segnosaurian hindfoot is prosauropod, not theropod in grade (Fig. 1). Early dinosaurs—lagosuchids and *Herrerasaurus*—also have a four-toed hindfoot, and many ornithischians retain this type (Fig. 1; Bonaparte, 1975; Reig, 1963). Most thecodonts differ greatly from segnosaurs and dinosaurs in general in having more supple, plantigrade hindfeet with a large, divergent fifth digit.

Skull—The segnosaur skull is also intriguing. It exhibits a kaleidoscopic blend of basal dinosaur, prosauropod, and ornithischian characters, but shows no distinctive theropod or thecodont attributes. The skull of *Erlikosaurus* shares with early theropods, prosauropods, and generalized ornithischians such general basal dinosaurian characters as a long, low profile, a tall, vertical quadrate, a slender tripronged jugal, a low triangular maxilla, and a broad lacrimal (Fig. 2). It also shares with early theropods and prosauropods an archaic archosaurian dentary–posterior mandible articulation in which the surangular overruns the dentary dorsally, and a slender quadrate process on both the squamosal and the quadratojugal (Fig. 2). That the skulls of the earliest representatives of the major predatory and herbivorous dinosaur groups—and the segnosaurs, too—are so similar both in overall design and in much of their detailed morphology is strong evidence of dinosaur monophyly. In contrast, no known thecodont skull shares more than a few isolated dinosaur-like characters with any of the genera pictured in Figure 1. In fact, all thecodonts have a robust, four-pronged jugal, a short, broad lacrimal, and (except for aetosaurs and phytosaurs) a down and backwards sloping quadrate and (except for aetosaurs) a tall, rectangular maxilla (Fig. 2; Walker, 1961; Ewer, 1965; Romer, 1972b). Because the segnosaurian skull also shares derived characters with both prosauropods and ornithischians, it further links these two groups together at a level above the thecodont grade.

The prosauropod-like characters in the skull of *Erlikosaurus* include the snout which has a large, similarly shaped premaxilla with a deep narial shelf, large, very elongate external nares, and a similarly shaped, tall, triangular maxilla with a tall, short, deeply recessed antorbital fossa and fenestra (Fig. 2). The mandibles of *Erlikosaurus* and *Plateosaurus* share a downwardly curved dentary, an anteriorly elongated splenial, a short, tongue-shaped prearticular, and a posteriorly deep mandible (Perle, 1979). In overall design and detailed morphology the skull of *Erlikosaurus* is remarkably similar to that of *Plateosaurus*. In build, the skull of *Erlikosaurus* is intermediate between the lightly built prosauropod and the stoutly constructed ornithischian skulls.

Erlikosaurus does not have three characters that most ornithischians do have, a closed mandibular fenestra, a predentary, and a coronoid process. However, a mandibular fenestra is present in fabrosaurid ornithischians (Thulborn, 1970), and even the predentary is of questionable significance. It has not been positively established that such morphologically archaic ornithischians as *Scelidosaurus, Parksosaurus,* the pachycephalosaurs, or certain nodosaurs have a predentary (Owen, 1861; Gilmore, 1924; Brown and Schlaikjer, 1943; Coombs, 1971; Galton, 1973b).

Early theropods (Fig. 2) contrast sharply with segnosaurs in having a shallow narial shelf on the premaxilla, small external nares, a very large, long antorbital fenestra and a small, shallow antorbital fossa, a straight or upwardly curved dentary, short splenial, long prearticular, and a moderately deep posterior mandible. The segnosaurian skull simply fails to share any derived characters with any theropod group, including the known Cretaceous genera. All thecodonts differ from segnosaurs in having a shallow narial shelf, a shallow or no antorbital fossa, and a straight or upcurved dentary (Fig. 2), and most thecodonts are predatory. Only aetosaurs differ from other thecodonts and share with segnosaurs and other herbivorous dinosaurs a deep posterior mandible, a large narial opening, and herbivory. However, aetosaurs differ from all the taxa discussed here in their aberrant "pig like" snout and constricted lateral temporal fenestra (Fig. 2).

Feeding Apparatus—Ornithischians are distinguished from all other archosaurs in having a highly derived food gathering and processing apparatus (Galton, 1973a). Food is cropped by a beak. Behind the beak, the presence of a mammal-like toothless space or diastema suggests that the food was shaped and passed backwards by a tongue supported by long hyoids, which positioned the foodstuffs in the tooth rows to be masticated. Food loss from the mouth was prevented by the cheeks (Fig. 2).

Two key characters are directly associated with the presence of cheeks in those dinosaurs that have them. One is the reduction of the rows of numerous, small foramina that supply nerves to the thin bands of cheek muscles (seen in lizards and most thecodonts, Fig. 2), into a few large foramina that pass large nerve bundles to the cheek muscles. The second character is the insetting of the tooth rows, so that they are bordered laterally by shelves which support the cheeks. The first character is the more important, because in mammals
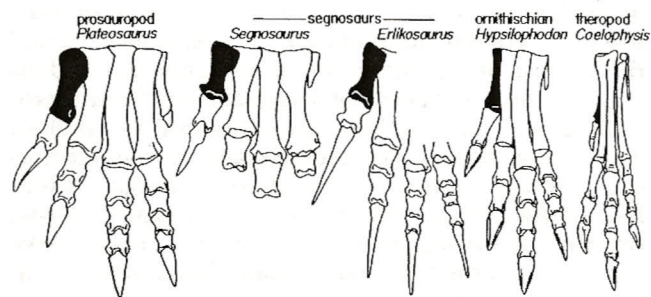

FIGURE 1. The left pes of basal dinosaurs and segnosaurs in anterior view. Metatarsal I in black. After Huene (1907), Raath (1969), Galton (1974), Barsbold (1979), and Barsbold and Perle (1979, 1980).
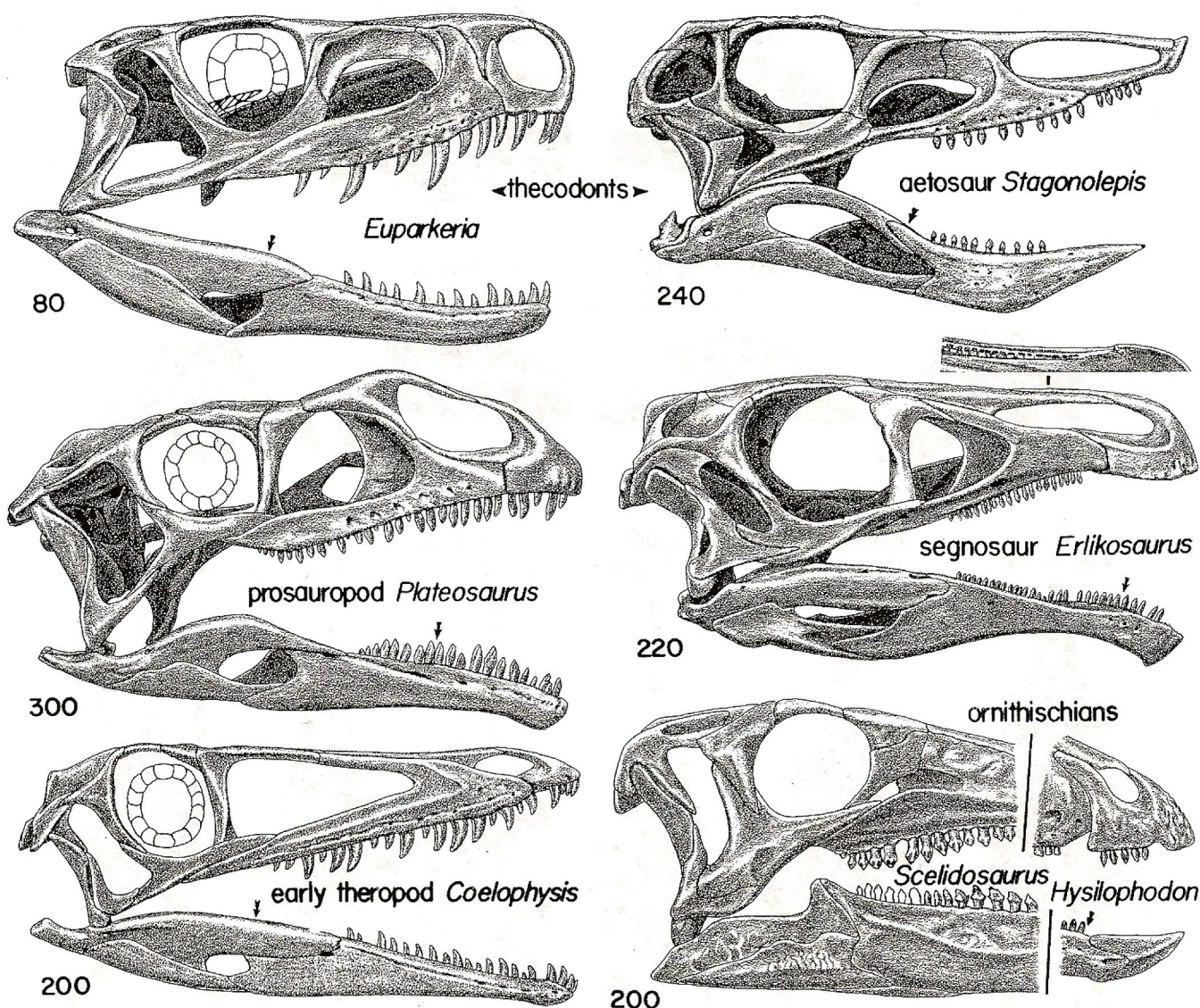
FIGURE 2. Skulls of theropods, early dinosaurs, and segnosaurs. The snout of *Scelidosaurus* is not known and that of *Hypsilophodon* is shown instead. Detail shows inset maxillary teeth of *Erlikosaurus*. Arrows indicate maximum anterior extent of cheek tissue as indicated by the anterior extent of the external mandibular shelf and the large nerve foramina. Number with each specimen indicates the approximate length (in mm) of upper jaw. In part after Owen (1861), Huene (1907), Walker (1961), Ewer (1965), Galton (1974), Barsbold and Perle (1980), and Perle (1981). *Plateosaurus* also after Amer. Mus. Nat. Hist. 6310, *Coelophysis* after Amer. Mus. Nat. Hist. 39018.

that have cheeks the nerve foramina are always large and few, but the lateral shelves are often not present. Theropods and the basal dinosaur *Staurikosaurus* lack both of these characters and are cheekless (Fig. 2; also Galton, 1977 and examination of the holotype of *Staurikosaurus,* MCZ 1669). Prosauropods, however, started to develop cheeks. In *Plateosaurus* there is a shelf running lateral to the sixth to ninth most posterior dentary teeth (Fig. 2). There are only one or two large nerve foramina on this shelf, suggesting that short cheeks covered the posterior-most teeth in *Plateosaurus*. Galton (1973a) suggests that the basal fabrosaurid ornithischians lack cheeks. But a shallow lateral shelf with a limited number of large nerve openings does parallel the maxillary tooth row in *Fabrosaurus* (see fig. 3 in Thulborn, 1970), suggesting that cheeks were present. In almost all other ornithischians, such as *Scelidosaurus* (Fig. 2), the lateral shelves are much more prominent and the cheeks were better developed.

Though *Erlikosaurus* lacks a predentary at the tip of its lower jaws, it has all the major ornithischian feeding adaptations. The premaxilla and anterior dentary lack tooth alveoli, and are sharply rimmed and heavily vascularized to support horned beaks (Fig. 2; see also Barsbold and Perle, 1979; Perle, 1981). A diastema separates the main tooth row from the upper
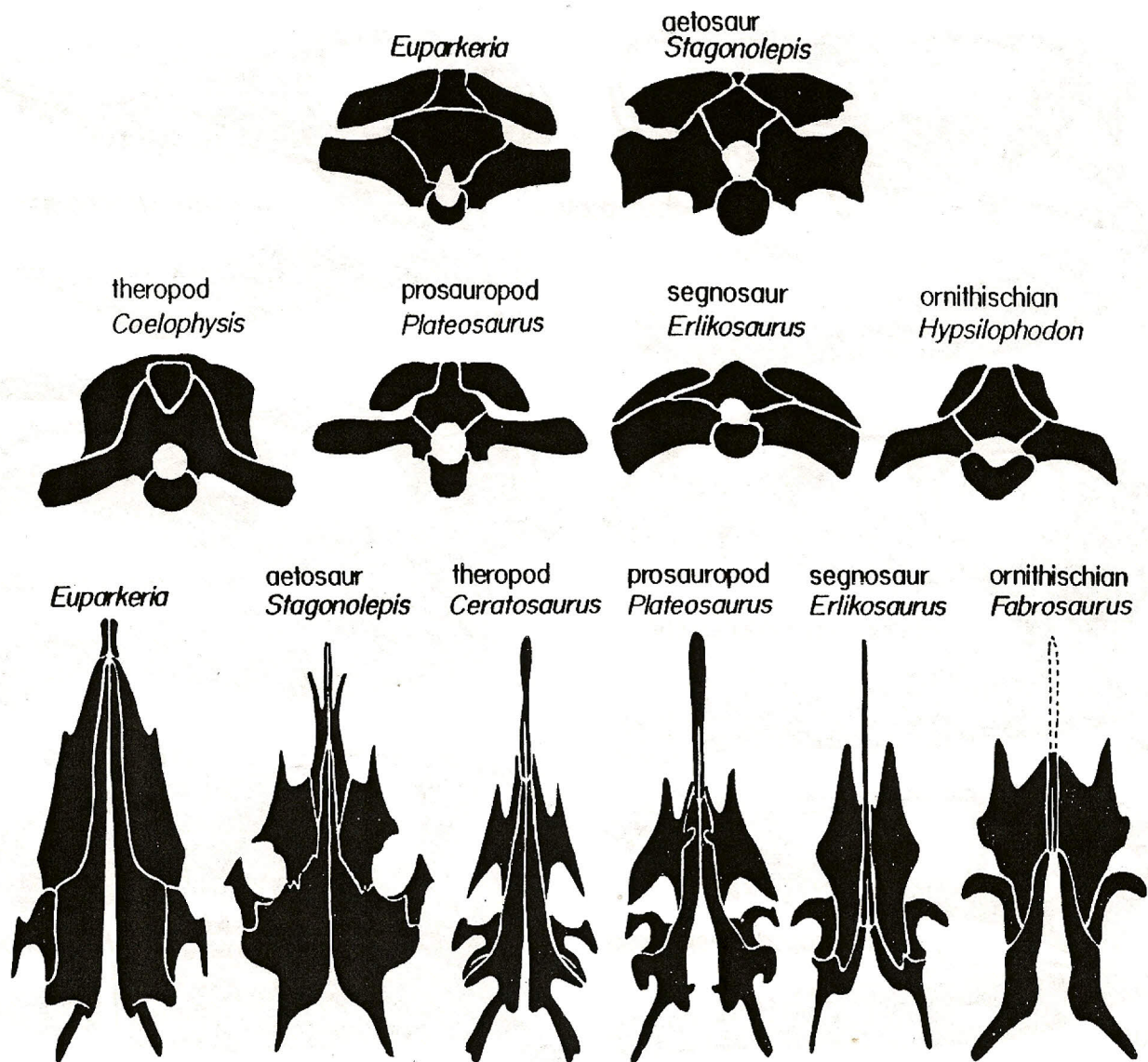
FIGURE 3. Occiputs in posterior view (top row) and palates in ventral view (bottom row) of thecodonts, early dinosaurs, and segnosaurs. Vomers of *Fabrosaurus* restored based on the skull length. In part after Huene (1907), Walker (1961), Ewer (1965), Thulborn (1970), Galton (1974), and Perle (1981).

beak, and another short diastema appears to separate the anterior-most dentary teeth from the main tooth row (Fig. 2). Cheeks were fully developed in *Erlikosaurus*. The tooth rows are inset (Fig. 2) and the anteriorly extending, shallow lateral shelves support cheeks that covered all but the most anterior dentary teeth. A few large foramina supplied these cheeks with large nerve bundles. Compared to prosauropods, *Erlikosaurus* could crop, manipulate, and masticate food in a more sophisticated, ornithischian-like manner. Among thecodonts only the herbivorous aetosaurs have a diastema separating the teeth from the beak (Fig. 2). However, in the details of this morphology aetosaurs differ greatly from segnosaurs. Also, aetosaurs lack cheeks because the dental foramina are small and numerous, and the tooth rows are not inset.

Palate—The roof of the mouth of *Erlikosaurus* is surprisingly like that of derived ornithischians, with very elongated, posteriorly shifted vomers that approach or contact the parasphenoid, posteriorly placed, narrow, highly vaulted palatines, and, most strikingly, ectopterygoids which run dorsally over the palatines, and posterior extensions of the maxillae which lock up under the maxilla–jugal contact (Fig. 3; Perle, 1981). This is surprising because the few known early ornithischian palates appear to be somewhat less derived in these characters than those of segnosaurians (Fig. 3; Thulborn, 1970). This suggests that in palatal characters segnosaurs are to a degree convergent with derived ornithischians. *Erlikosaurus* does have a most untheropodous palate—significantly, it lacks the "carnosaurian pocket" found under the ectopterygoids of

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almost all theropods. All thecodonts differ from segnosaurs in having shorter, broader, separate vomers, and larger, more heavily built pterygoids (Fig. 3).

Braincase—*Erlikosaurus* has an unusual braincase in that the basisphenoid is grossly expanded into an intensely pneumatized bulbous structure (Perle, 1981). However, the occipital face is that of a herbivorous dinosaur in appearance—low, with small posterior parietals, a dorsally placed supraoccipital, elongated, narrow opisthotic wings, and, as in ornithischians, a closed post-temporal fenestra (Fig. 3). Theropods also have the latter character, but have none of the other features (Fig. 3). Most thecodonts have taller occiputs with large parietals, a lower supraoccipital, shorter, broader opisthotic wings, and a large post-temporal fenestra (Fig. 3). *Erlikosaurus* has a fenestra pseudorotunda, a middle ear structure also found in prosauropods and theropods (Paul and Carpenter, in preparation), ornithischians (Perle, 1981; Sues, 1980; Brett-Surman and Paul, in press), and phytosaurs (Camp, 1930). This contradicts assertions that dinosaurs and thecodonts lacked this structure (Whetstone and Martin, 1979, 1981).

Teeth—Those arguing for dinosaur monophyly have stressed the similarity of the distinctive, constrictedwaisted and expanded–crowned teeth of prosauropods and early ornithischians (Bakker and Galton, 1974; Bonaparte, 1976). *Erlikosaurus,* too, has this type of tooth (Barsbold and Perle, 1979; Perle, 1979, 1981). Among the thecodonts only aetosaurs have similar teeth (Walker, 1961). Theropods and most thecodonts are very different in having blade-crowned, straight-rooted teeth.

Postcrania—Segnosaurs are typically dinosaurian in skeletal morphology, short-trunked, with long, fully erect, cylindrically jointed limbs. This is completely different from thecodonts which are long-trunked, lowslung animals with semierect, complexly jointed limbs.

Forelimb—Like the pes, the segnosaurian forelimb with its semicircular scapulocoracoid, down and backwards facing glenoid, and a large, rectangular, deltopectoral crest represents a basal dinosaurian grade that otherwise is found in lagosuchids, early theropods, prosauropods, and *Heterodontosaurus* (Fig. 4), but not in thecodonts. This forelimb design grade is also found in the Late Cretaceous *Therizinosaurus* (Barsbold, 1975), a Mongolian specimen of unknown affinities, and a humerus assigned—perhaps incorrectly—to the Late Cretaceous Mongolian tyrannosaurid *Alectrosaurus* (Gilmore, 1933; Perle, 1977).

Pelvis and Hindlimb—The segnosaur pelves blend ornithischian, sauropod, and unique characters into a very unusual design. The pubis is retroverted and lacks an anterior process (Fig. 4). The ilia are sauropod-like in having a very deep, laterally flaring anterior blade (Perle, 1979). This probably represents convergence with sauropods in order to support a massive, fermenting gut for processing ingested fodder. The retroverted pubis is of course the ornithischian condition and may be expected in a proto-ornithischian (Fig. 4). But retroverted pubes are also seen in the basal di
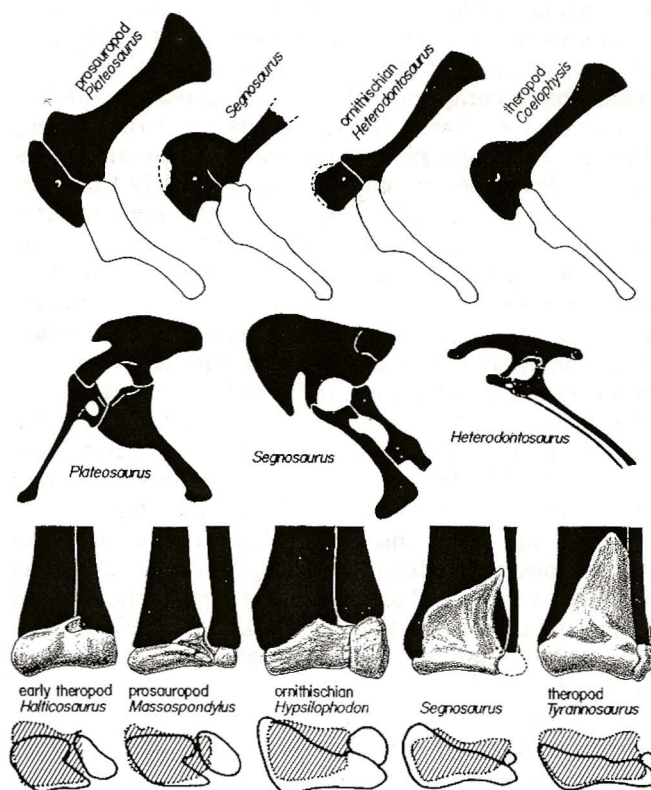

FIGURE 4. The left scapulocoracoid and humerus (top row), pelvis in left lateral view (second row), the left articulated tibia, fibula, astragalus, and calcaneum in anterior view (third row) and in distal view (fourth row, astragalus hatched, calcaneum removed) of various dinosaurs compared to segnosaurs. In part after Huene (1907), Lambe (1917), Raath (1969), Galton (1974), Barsbold (1979), Perle (1979, 1981), Barsbold and Perle (1979, 1980), Santa Luca (1980), and Cooper (1980, 1981).

nosaur *Herrerasaurus* (unbroken MCZ uncataloged specimen), the sauropod *Nanshiungosaurus* (Dong, 1979), velociraptorids and other derived theropods close to bird ancestry (Barsbold, 1979), *Archaeopteryx,* and in birds themselves. No thecodont had a retroverted pubis.

It is important to note that the retroverted pubis of segnosaurs is significantly closer to those of ornithischians than to those of the bird-like theropods and birds. In the protobird-bird clade the pubic peduncle of the ilium is retroverted in the same direction as the pubis (Barsbold, 1979). In segnosaurs and ornithischians the pubic peduncle is not retroverted in the same line as the pubis; instead it points forwards (Fig. 4). *Herrerasaurus* also has the latter kind of pubic peduncle; in fact, a forward pointing pubic peduncle is the general archosaur condition.

The *Segnosaurus* ankle is both interesting and perplexing. It is ornithischian-like in having a deep lateral malleolus of the tibia that backs the fibula distally, reduced astragalar condyles that only partly cover the distal tibia, and a tall triangular ascending process (Fig.

4). This is perplexing because the segnosaurian ankle is more derived than those of some ornithischians—*Pisanosaurus, Scelidosaurus,* and *Thescelosaurus*—which have comparatively archaic, prosauropod-like ankles (Fig. 4; Owen, 1861; Bonaparte, 1976; Galton, 1974a). This suggests that the segnosaurian ankle was in part developed parallel to and separately from the true ornithischian ankle. Like segnosaurs, derived theropod astragali also have a tall ascending process and a lateral malleolus that backs the fibula. However, theropods differ greatly in the details of these characters (Fig. 4). Also, as theropods evolved these characters long after they developed a tridactyl foot, this represents a development independent of segnosaurians. Some thecodonts such as *Euparkeria* have fairly simple ankles suitable for ancestry of the mesotarsal dinosaur ankle. However, most thecodonts, including aetosaurs, have complex crurotarsal ankles that require a major functional and morphological reversal to become dinosaurian. It has been suggested that variations in "peg in a socket" astragalar–calcaneal articulations delineate archosaur clades (Cruickshank, 1979; Thulborn, 1980; Chatterjee, 1982). Whether segnosaurs have a "peg in a socket" articulation is not clear, and within the Ornithischia this character varies between closely related groups (Brett-Surman & Paul, in press). Indeed, whether any dinosaur has a true peg in a socket articulation is questionable (Cooper, 1980), and such single character phylogenies are of dubious value.

DISCUSSION

The unimportance of a taxon's temporal placement in regards to its interrelationships with other taxa is often overemphasized in cladistics. However, segnosaurs are a case where the rule applies. The segnosaurian skeleton represents a prosauropod grade archosaur in snout, mandible, and hindfoot morphology, an ornithischian in cheek, palate, pubis, and ankle morphology, and is early dinosaurian in other aspects of its morphology. As Late Cretaceous dinosaurs, the segnosaurs are disquietingly out of their temporal place; except for a few specializations, archosaurs of their morphological grade would fit comfortably into Late Triassic strata. They appear to be survivors of the early dinosaur radiation. The alternative, that segnosaurians are derived from theropods, is possible. But a cladistic analysis does not support this hypothesis because segnosaurs share no derived characters with theropods that they do not also share with other dinosaurs, are very different in many aspects of their morphology from theropods, and are more archaic than theropods in many regards (Fig. 5B[2]). Deriving segnosaurs from derived velociraptorid theropods incurs 5 reversals and 20 convergences with other herbivorous dinosaurs.

Also possible, but even less feasible, is the possibility that segnosaurs are derived from thecodonts independently of other dinosaurs. It is interesting that no cladogram has been published that uses the whole skeletal morphology of archosaurs to detail the polyphyletic evolution of various dinosaur groups from various the-codont groups. I will not attempt to do so here. However, a cladogram testing the polyphyletic origin of herbivorous dinosaurs from thecodonts using 45 characters is presented in Figure 5A. Euparkerid thecodonts are the outgroup. Prosauropods are derived separately from aetosaurs, and since aetosaurs share some characters with segnosaurs and ornithischians the two dinosaur groups are derived independently from aetosaurs. Many other cladograms polyphyletically deriving dinosaurs from thecodonts could be constructed, but all would probably suffer from the same problems that afflict this one. An extraordinary degree of convergence between the dinosaur groups is postulated. Segnosaurs show 22 triple convergences and 11 double convergences with other herbivorous dinosaurs (Fig. 5A)—this when no known thecodont group shares with segnosaurs major derived characters *that are not found in other dinosaurs or thecodonts.* Indeed, segnosaurs differ greatly in almost all details of their morphology from all known thecodonts, including aetosaurs. All herbivorous dinosaurs and theropods differ greatly from thecodonts. Lastly, deriving any dinosaur from any crurotarsal thecodont group, such as aetosaurs, invokes a major reversal in morphology. In all, segnosaurs show six major reversals from aetosaur morphology.

Convergence occurs constantly in evolution. But invoking massive convergence to explain relationships when few or no shared derived characters are present to confirm the suggested relationship misses the point. Rigorous phylogenetics attempts to arrive at a "best fit" hypothesis that minimizes convergence, major reversals, and imaginary ancestral groups while maximizing the number of shared derived characters within each hypothesized clade.

By these criteria, the most parsimonious explanation of segnosaur origins is that they are monophyletic with all the dinosaur groups. Constructing such a cladogram is a straightforward task (Fig. 5B[1]). Fifty characters are considered, euparkerids are the outgroup, and aetosaurs are derived independently from dinosaurs. This cladogram is a short version of more complete analyses of the archosaurs in Paul (1984), and in preparation by Bakker and Paul. A trichotomy exists between early dinosaurs, theropods, and prosauropods because the former are the most suitable ancestors for both theropods and prosauropods, but the derived foot of theropods and derived skulls of prosauropods make these two groups unsuited as ancestors for each other.

The cladogram works well, in part because segnosaurs share 30 derived characters with other dinosaurs that are absent from all thecodonts. The structural similarities are especially strong because they are detailed, formed by homologous units, and extend throughout the skeleton. No major reversals occur in deriving segnosaurs from early dinosaurs. Major imaginary ancestral types are avoided. Finally, convergence between segnosaurs and thecodonts is not eliminated, but is kept to a minimum with only six convergences with the aetosaurs, and another four with theropods.
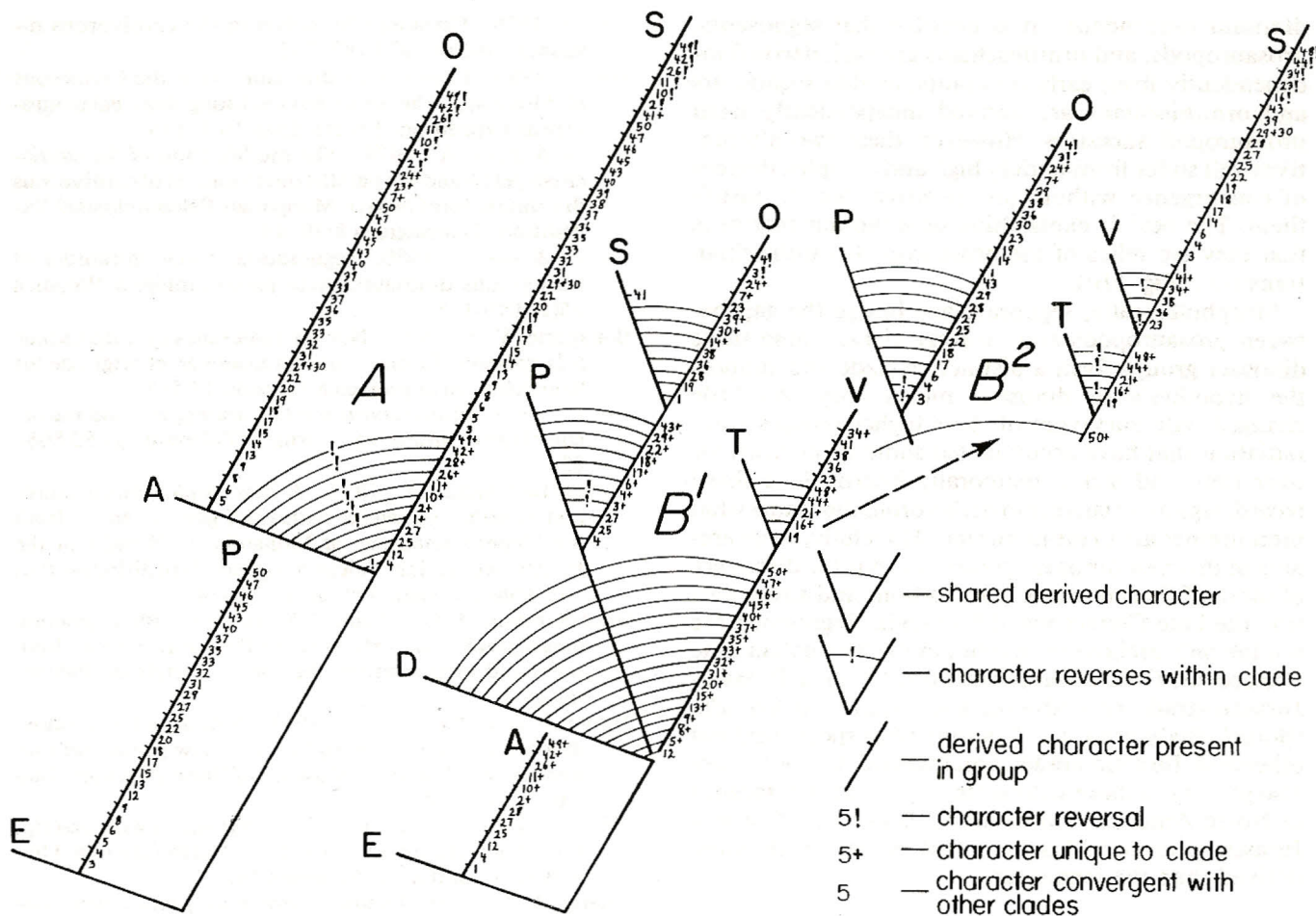
Working from the premise that segnosaurs are early

FIGURE 5. Cladograms testing: *A*, the polyphyletic evolution of herbivorous dinosaurs and segnosaurs from thecodonts; *B¹*, the monophyletic evolution of herbivorous dinosaurs and segnosaurs from basal dinosaurs; and, *B²*, derivation of segnosaurs from theropod dinosaurs independently of herbivorous dinosaurs. Euparkerid thecodonts are the outgroup. E, euparkerids; A, aetosaurs; D, early dinosaurs—lagosuchids, lewisuchids, staurikosaurs, herrerasaurs; P, prosauropods; S, segnosaurs; O, ornithischians; T, early coelophysid theropods; V, derived velociraptorid theropods. List of characters (outgroup condition in parenthesis); 1, beaked (not beaked); 2, premaxilla "pig snouted" (premaxilla normal); 3, premaxillary shelf beneath external nares large (same shallow); 4, external nares large (same moderate in size); 5, antorbital fossa expanded antero-ventrally (antorbital fossa narrow antero-ventrally); 6, antorbital fossa deeply recessed (same shallow); 7, antorbital fenestra and fossa very reduced (same are large); 8, lacrimal tall, anterior process short, slender (lacrimal short, anterior process long, massive); 9, jugal 3 pronged, antorbital process is absent (jugal 4 pronged, antorbital process is present); 10, lateral temporal fenestra nearly closed (same large and normal); 11, superior temporal fenestra faces laterally (same faces dorsally); 12, quadrate vertical (quadrate slopes down and backwards); 13, vomers elongated, narrow, and coalesced (vomers shorter, broad, and separate); 14, vomer-pterygoid articulation and the palatine sited posteriorly (same sited more anteriorly); 15, pterygoids slender (pterygoids robust); 16, ectopterygoid bears "carnosaurian pocket" (ectopterygoid lacks same); 17, occiput flattened (occiput tall); 18, parietals reduced (parietals large); 19, post temporal fenestra closed (same open); 20, opisthotic wings elongated, narrow (same short, broad); 21, dentary straight (dentary curved upwards); 22, dentary curved downwards (dentary curved upwards); 23, surangular does not overrun dentary (surangular overruns dentary); 24, coronoid process present (same absent); 25, mandible posteriorly deep (same shallow); 26, mandibular fenestra very large (same moderate in size); 27, teeth constricted waisted, spatulate crowned (teeth are straight rooted blades); 28, diastema present (diastema absent); 29, cheeks partly developed (cheeks absent); 30, cheeks fully developed (cheeks absent); 31, neck "s" flexed (neck straight); 32, clavicle-interclavicle brace absent (same present); 33, coracoid elongated (coracoid short and broad); 34, scapula is a slender strap (scapula blade is broad); 35, inner manus digit medially divergent (same is straight); 36, opisthopubic (pubis not retroverted); 37, deltopectoral and cnemial crests large (same crests are small); 38, lateral malleolus of tibia backs fibula (same does not back fibula); 39, main body of astragalus reduced, tibia forms part of articular surface for pes (astragalus large and forms entire proximal portion of joint); 40, ascending process of astragalus tall, backed by tibia (same short, lies under tibia); 41, ascending process of astragalus very tall, backed by tibia (same short, lies under tibia); 42, ankle crurotarsal (ankle essentially mesotarsal); 43, pedal digit I and claw enlarged (same moderate in size); 44, pedal hallux present, foot tridactyl (metacarpal I articulates with ankle, foot tetradactyl); 45, pedal digit V very reduced and nondivergent (same very large, divergent); 46, pes fully digitigrade (pes plantigrade); 47, stance fully erect, limb joints cylindrical (stance semierect, multiaction joints); 48, stance obligatorily bipedal (stance basically quadrupedal); 49, heavily armored (armored lightly); 50, not armored (armored lightly). Data sources not already cited are Romer (1972a) and Galton (1977).

dinosaur descendants, it is possible that segnosaurs, prosauropods, and ornithischians are each derived independently from early dinosaurs, or that segnosaurs and ornithischians are derived independently from prosauropod ancestors. However, these two alternatives still suffer from unduly high and complex degrees of convergence without any positive data to justify them. The best fit explanation of segnosaur origins is that they are relics of the prosauropod–ornithischian transition (Fig. 5B[1]).

Morphologically, segnosaurians bridge the gap between prosauropods and ornithischians. These three dinosaur groups form a distinctive clade and support the hypothesis of dinosaur morphology. As little changed, late survivors of their higher group's early radiation that have accumulated some specializations over time and lack a temporally intermediate fossil record, segnosaurians are to herbivorous dinosaurs what monotremes are to the mammals. Hopefully, an awareness of this new dinosaur group will spur the discovery of more of their remains in collections and strata outside the Late Cretaceous of Mongolia. Segnosaurs are not the only archosaurian relics in the Mongolian Late Cretaceous. *Gobisuchus* (Osmólska, 1972), a Triassic–Jurassic-grade crocodiloid, and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), a somewhat specialized but otherwise Jurassic grade camarasaurid sauropod, are also present in these sediments. In the Late Cretaceous of North America, *Parksosaurus* is another Triassic–Jurassic-grade ornithischian that is not much more derived than the segnosaurs.

CONCLUSION

Because segnosaurians almost certainly are neither theropods nor their descendants, they are here formally removed from the Theropoda. Lacking a predentary, the segnosaurians do not meet a major definition of the Ornithischia (Seeley, 1887). Nor does the traditional classification of dinosaurs recognize the possibility of their monophyly. Until a new, rigorously defined systematic ordering of the dinosaurs is available, the segnosaurians should be considered a clade of the Dinosauria intermediate between prosauropods and ornithischians.

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