

# The Dinosaurs of Transylvania

DAVID B. WEISHAMPEL, DAN GRIGORESCU, AND DAVID B. NORMAN

## Dinosaurs of Transylvania: Island Biogeography in the Late Cretaceous

*Despite early work on the Late Cretaceous (latest Maastrichtian) fauna of the Hațeg region of Transylvania, this assemblage has been underutilized in terms of its importance to dinosaur systematics, European paleoecology, and global paleobiogeography. The depositional environments of the Hațeg localities consist principally of alluvial fans and braided rivers. The region itself was one of many volcanic islands distributed within a broad European archipelago system. The Hațeg fauna is dominated by dinosaurs, in particular *Telmatosaurus*, *Rhabdodon*, and "Struthiosaurus." A preliminary assessment of their systematics suggests that *Telmatosaurus* is the most primitive hadrosaurid, *Rhabdodon* is a euornithopodan of uncertain affinity, and "Struthiosaurus" is one of the more primitive nodosaurids. In combination, phylogenetics, tectonics, and sedimentology suggest that the distribution of these Transylvanian taxa is due to dispersal rather than vicariance.*

Figure 1.  
*Telmatosaurus transylvanicus*.  
BRIAN FRANZAK

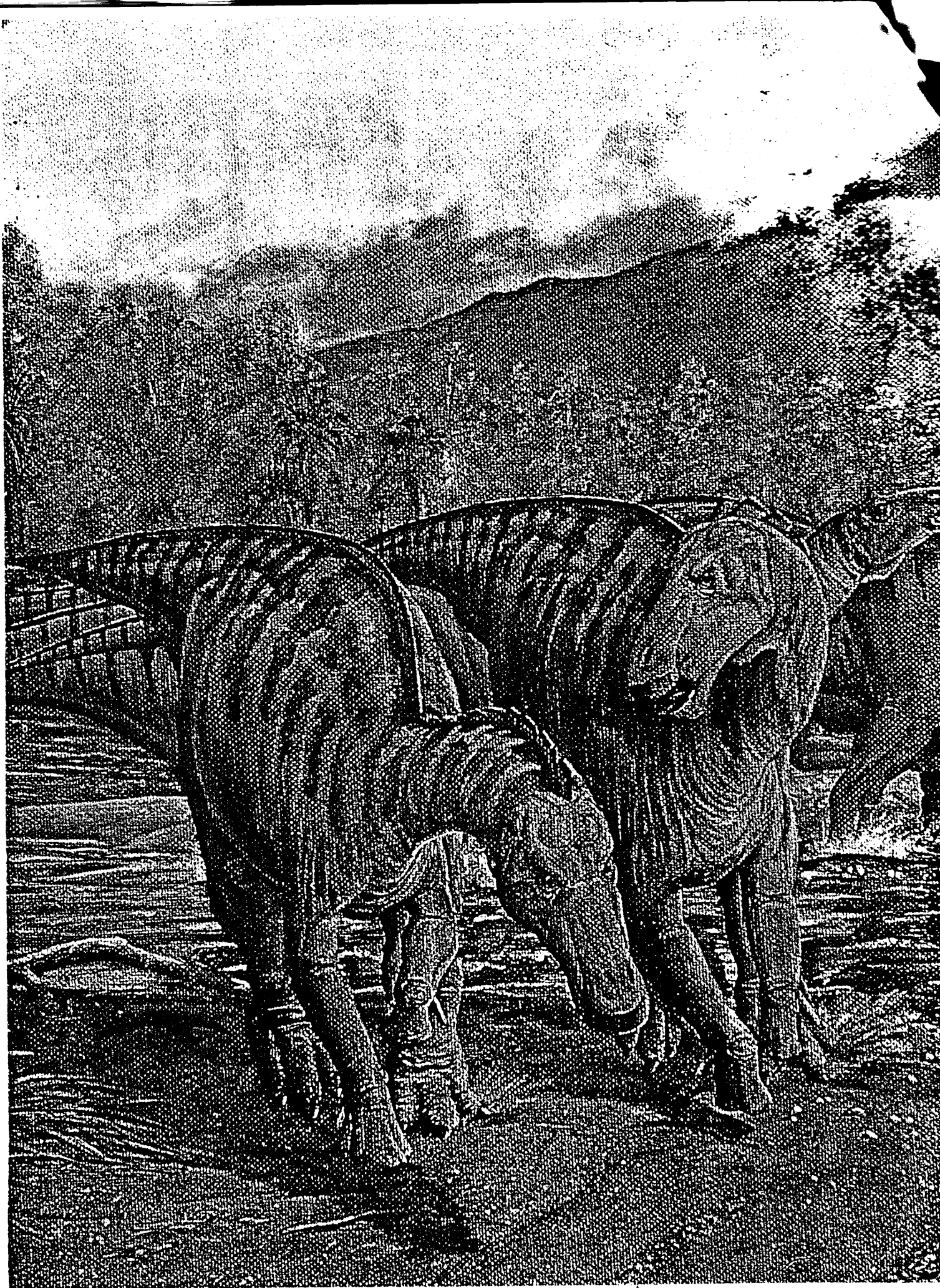
**T**O THE GENERAL PUBLIC Transylvania conjures up images of Count Dracula, but to dinosaur paleontologists it is an area where some of the most interesting, albeit poorly studied, dinosaurs lived toward the end of the Mesozoic. The remains of these animals are found in the area south of the village of Hațeg (pronounced Hat-zeg) in Judetul Hunedoara (Hunedoara County) (Figure 2).

Paradoxically, this small region in central Europe assumes great importance for our understanding of some of the closing moments of dinosaur evolution. The last phases of dinosaur evolution are best recorded during the Late Cretaceous, particularly for the Campanian and Maastrichtian ages (83 to 65 Ma BP<sup>28</sup>) and principally from Laurasia (i.e., the Northern Hemisphere). Within Laurasia, the vast majority come from either western North America or eastern Asia.<sup>19,74,79</sup> Few European faunas contemporary with those of North America and Asia (Figure 3) have produced more than modest faunas. The Hațeg fauna is the most diverse and best preserved of these European assemblages and hence the most readily comparable to those of Asia and North America. Moreover, the Hațeg localities, along with the other contemporary European sites, are distributed among chains of islands in an archipelago in an otherwise marine-dominated Europe. The context of Transylvania as an island provides a paleontological arena for testing hypotheses about dwarfism, atavism, and retention of primitive features through systematics, paleoecology, geology, and geochronology. Here we consider whether dispersal (distribution owing to animal movement) or vicariance (distribution owing to geographic alteration) can account for the occurrences of three dinosaur taxa—*Telmatosaurus*, *Rhabdodon*, and "Struthiosaurus."

### HISTORY OF WORK ON THE HAȚEG FAUNA

In the late 1890s, Ilona Nopcsa discovered fossil reptile material on the family estate near Szentpéterfalva in the Austro-Hungarian Empire (now Sînpetru, Romania). Her brother, Franz Baron Nopcsa, took up the study of these and other specimens from the Hațeg Basin. Under the direction of E. Suess, Nopcsa excavated and studied the material, and presented the first results before the Viennese Academy of Science on 21 June 1899.<sup>45,78</sup> The only other early collections from the Hațeg Basin were made by Kadic O. in 1914 for the Hungarian Geological Survey in Budapest; Nopcsa<sup>50</sup> later studied this collection.

From the close of World War I until the 1970s, virtually no paleontological collecting took place in the Hațeg Basin. Since the late 1970s, a team of the Facultatea de Geologie i Geofisica from the Universitatea





Bucuresti has collected regularly. The results include a large collection containing most of the taxa described by Nopcsa, as well as a number of new forms, including small and large theropods, multituberculate mammals, and a dinosaur nesting site found near Tuștea in the northern part of the Hațeg Basin. In addition to the collection of fossil material, taphonomic, stratigraphic, and sedimentologic studies have been conducted over the entire basin. The information obtained provides a detailed characterization of the Late Cretaceous paleoenvironments in the Hațeg Basin, a first step to a wider paleogeographic reconstruction of the area (Figure 1).

## Geology and Paleocology of the Hațeg Basin

Throughout the Late Cretaceous, Europe was covered by a shallow sea studded with a dozen or more volcanic islands (Figure 4).<sup>20</sup> The largest of these islands (~10 000 000 km<sup>2</sup>) was on what is now the Transpyrenean region. Many smaller islands (~100 000 km<sup>2</sup>) were farther to the east in a zone now comprising Austria, Czechoslovakia, Hungary, Romania, Bulgaria, and the Caucasus. The "Hațeg" island (~7500 km<sup>2</sup>) was in the midst of this archipelago, 200 to 300 km from neighboring islands.

Collectively, these islands were formed as a result of complex plate movement in the Mesozoic Tethyan Realm, ultimately controlled by counterclockwise rotation of the African continental plate.<sup>20</sup> In the east, closure of the Tethyan Basin via subduction along its northern margin produced a number of island arcs in what is now the Middle East and the Caucasus. In addition, subduction of Tethyan oceanic crust under the more southerly Arabian portion of the African continental plate formed an island chain across present-day southern Iran. Closure of this arm of the Tethys was complete ~25 Ma ago.

In the west, complex motion involving the Iberian plate (present-day Spain and Portugal) and the Apulian microplate (roughly the Adriatic region of south-central Europe<sup>12,17</sup>) provided a regional environment for island arc formation in a belt from eastern Spain through south-central Europe. The "Hațeg" island, like other islands within this chain, was formed as the product of crustal movement north of the African continental plate. During the Early Cretaceous, Apulia separated from the northern margin of the African plate along a spreading zone directly north of the Mediterranean margin of Africa. This microplate consisted of thick continental crust, capped virtually entirely by marine carbonates. As Apulia was pushed northward, as a consequence of both oceanic spreading and counterclockwise rotation of the African plate,<sup>80</sup> it overrode the Carpathian deep-sea basin.<sup>71</sup> This subduction and the resulting volcanic activity produced the island system (including the "Hațeg" island) along the leading edge of the Apulian microplate.

Topographically, the Hațeg region is an intramontane basin formed ~68 Ma ago (Figure 5). The basin is ~45 km long from east to west, bounded by the Sureanu (Sebes) Mountains in the northeast, Poiana Ruscă in the northwest, and the Retezat Mountains in the south. Narrow zones of crystalline basement rock separate the Hațeg Basin from two other intramontane basins: in the east, the Petrosani Basin (Oligocene and Lower Miocene freshwater lacustrine and brackish deposits) and, in the west, the Ruscă Montana Basin (Upper Cretaceous marine and lacustrine deposits,

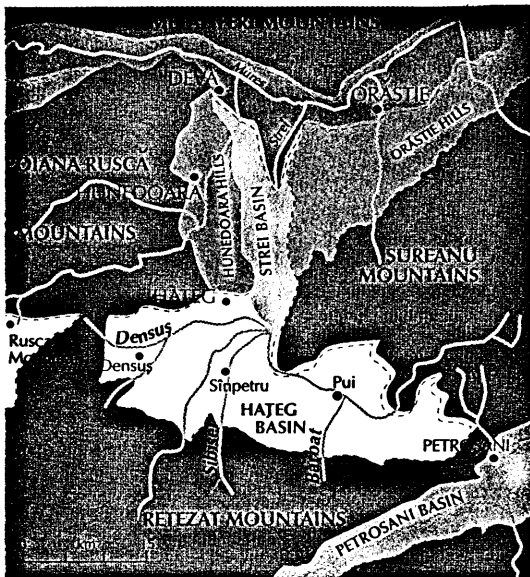


Figure 2 (top).  
The Hațeg region of Transylvania.

Figure 3 (bottom).  
Major geologic features surrounding the Hațeg Basin.

REDRAWN FROM DAN GRIGORESCU

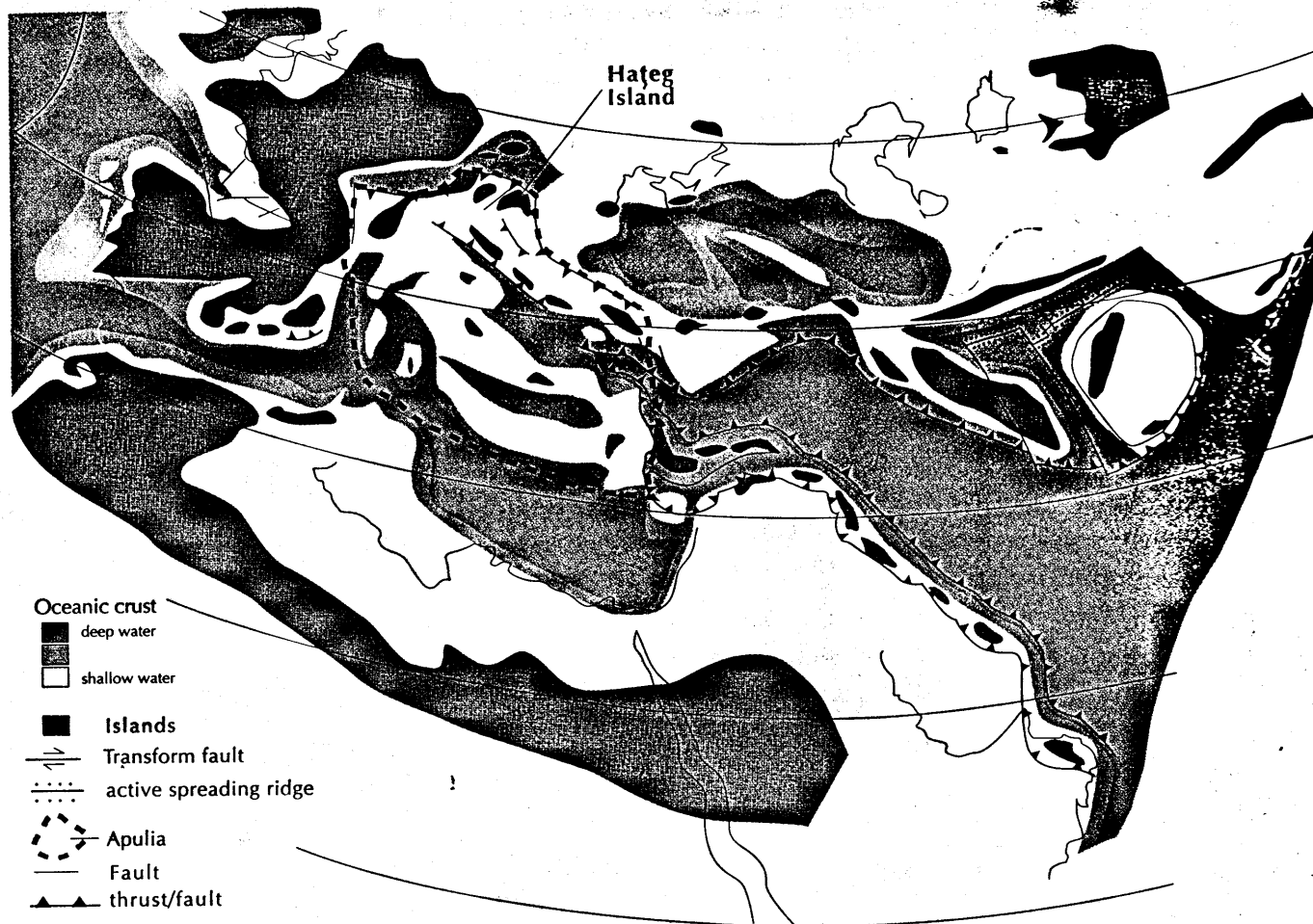


Figure 4.  
Paleogeographic map of Europe during  
latest Cretaceous time (ca. 65 Ma BP).  
ADAPTED FROM DERCOURT AND COLLEAGUES.<sup>20</sup>

the latter including coal intercalations and a rich continental flora). The north-central part of the Hateg Basin communicates with the Mures Trough, the southwestern limit of the large Intracarpathian Depression of Transylvania, as well as the geologic boundary between southern and western Carpathians.

The upper Maastrichtian continental deposits outcrop only along the western part of the Hateg Basin. A short marine transgression (middle Eocene) interrupted the general trend of continental sedimentation, thereby dividing the continental deposits into two cycles: an upper Maastrichtian-lower Eocene, and an upper Eocene-Miocene. The latter consists of red facies with intercalations of gray lacustrine limestones that outcrop in the south-central part of the basin. Although these beds have often been erroneously correlated with strata of similar lithology beneath the marine transgression, a molluscan assemblage provides an Oligocene date for the post-transgressive sequence.<sup>41</sup>

The Transylvanian dinosaur fauna comes from strata under beds deposited during the Eocene transgression. These continental deposits are exposed in two regions within the western part of the basin. Each exhibits distinctly different lithologies and hence depositional environments. The Sînpetru Formation outcrops in the central part of the southern end of the basin, and the Densus-Ciula Formation in the north.<sup>26</sup>



















#### SÎNPETRU FORMATION

The Sînpetru Formation has yielded the majority of fossil vertebrates from

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-  Dinosaur bones
-  Dinosaur eggs
-  Problematic K/T boundary
-  Andesitic dykes
-  Quaternary deposits
-  Upper Miocene brackish deposits
-  Middle Miocene (Badenian) deposits
-  Upper Paleogene - Lower Miocene continental deposits
-  Uppermost Cretaceous - Lower Paleogene continental deposits
-  A—Sînpetru Formation
-  B—Densus-Ciula Formation
-  a—lower member
-  b—upper member
-  Cretaceous marine deposits
-  Proterozoic and Paleozoic metamorphic rocus
-  Fault
-  Overthrust
-  Stratigraphic limit

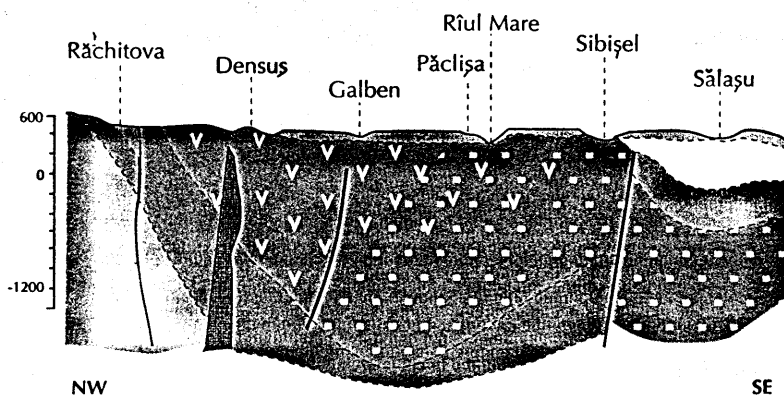
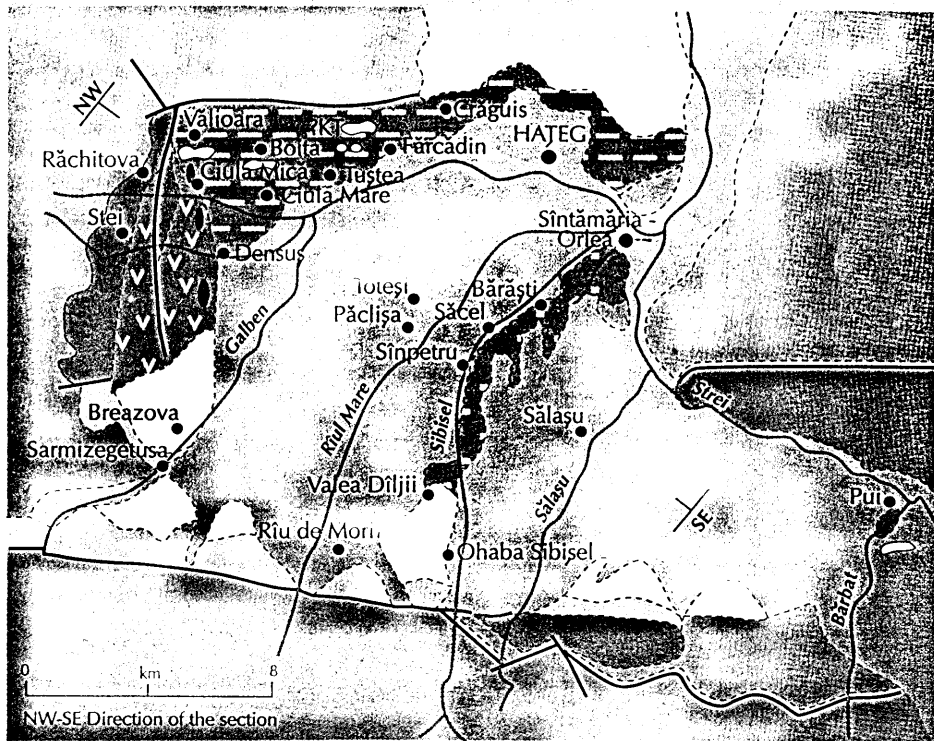


Figure 5 (above).  
 Geology of the Hațeg region, Judetul Hunedoara, Romania. Upper: Geologic map of the western part of the Hațeg Basin. Lower: Geologic section of the western part of the Hațeg Basin.  
 REDRAWN FROM DAN GRIGORESCU

Figure 6 (right).  
 Outcrop of the Sînpetru Formation on the western bank of the Sibișel River near the village of Sînpetru.  
 DAVID B. NORMAN



the Hațeg Basin. It outcrops on both sides of the Sibîșel Valley (Figure 6), where it is at least 2500 m thick. The formation consists almost exclusively of clastic sediments ranging from coarse conglomerates (rudites, including pebbles 15 to 20 cm in diameter) to shales (lutites). Poorly cemented sandstone components predominate, forming massive, poorly sorted, fining-upward sequences. The Sînpetru Formation also includes irregular caliches and tuffites comprising a mixture of fine terrigenous material and volcanic ash. Together, these beds are grouped in cyclic sequences that range from 1 to >3 m thick.

Sediments of the Sînpetru Formation were deposited within a braided river environment. These braided rivers probably developed in the lower parts of an alluvial fan system that was part of the gentle north-facing slope of the Retezat piedmont. The generally poorly sorted and graded strata then become a consequence of the rapid discharge of the mixed bedload of sand and gravel from the stream channels within the depositional system. Furthermore, the fine-grained, burrowed sediments and caliches formed adjacent to the streams during dry periods. These overbank deposits also yield fossil vertebrate material.

The last depositional phase is marked by a shift in lithology. The frequency and size of conglomeratic pebbles increase toward the top of the unit, andesitic tuffites become more common, and the finer grained beds virtually disappear. These shifts reflect a major increase in uplift and erosion rates and an escalation of subduction along the northern margin of Apulia and consequent volcanism to the northwest of the Hațeg region.

The age of the Sînpetru Formation is currently based on palynology and molluscs. An association of gastropods collected at Sînpetru<sup>2</sup> supports a Late Cretaceous age for the formation. The upper portion of subjacent strata is early Maastrichtian in age;<sup>62</sup> accordingly, the basal age of the Sînpetru Formation is probably late Maastrichtian. Based on the general stratigraphic context of the basin, the upper portions of the formation may merge into the Paleocene.

#### DENSUȘ-CIULA FORMATION

The ~4000-m-thick Densuș-Ciula Formation covers a large area of the northwestern part of the Hațeg Basin. At the base of the Densuș-Ciula Formation is a 1.5-m-thick, massive, conglomerate bed with volcanic intercalations. This unit forms an angular unconformity with underlying marine deposits of Campanian-early Maastrichtian age.

The Densuș-Ciula Formation is divided into two unnamed members.<sup>26</sup> The gray-colored lower member consists of repetitive, asymmetric sequences of volcanic and terrigenous strata. The upper member is dominated by red terrigenous rocks ranging from coarse conglomerates to mudstones and shales.

The lower member of the Densuș-Ciula Formation constitutes alluvial fan deposition near or along the flanks of volcanoes. Proximal facies include the coarsest and the most poorly sorted sediments and these grade into mid-fan and distal-fan facies consisting of somewhat finer-grained units (including cross-bedded channeled conglomerates), debris flows, and better-sorted sands and silts of sheetflood origin. Lastly, the alluvial fan deposits merge into lacustrine facies represented by mudstones, shales, and horizontally laminated tuffites. Alluvial fan sedimentation was periodically interrupted by ash-fall deposition and by lahar mudflows, indicated by the structureless matrix that supports the conglomerate pebbles.<sup>1</sup> The

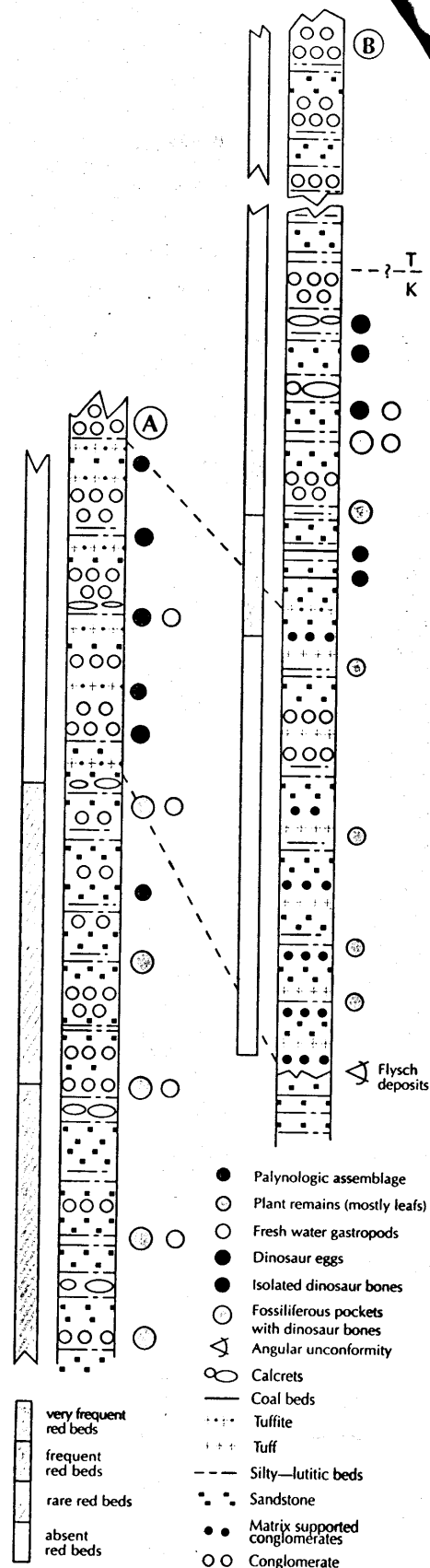
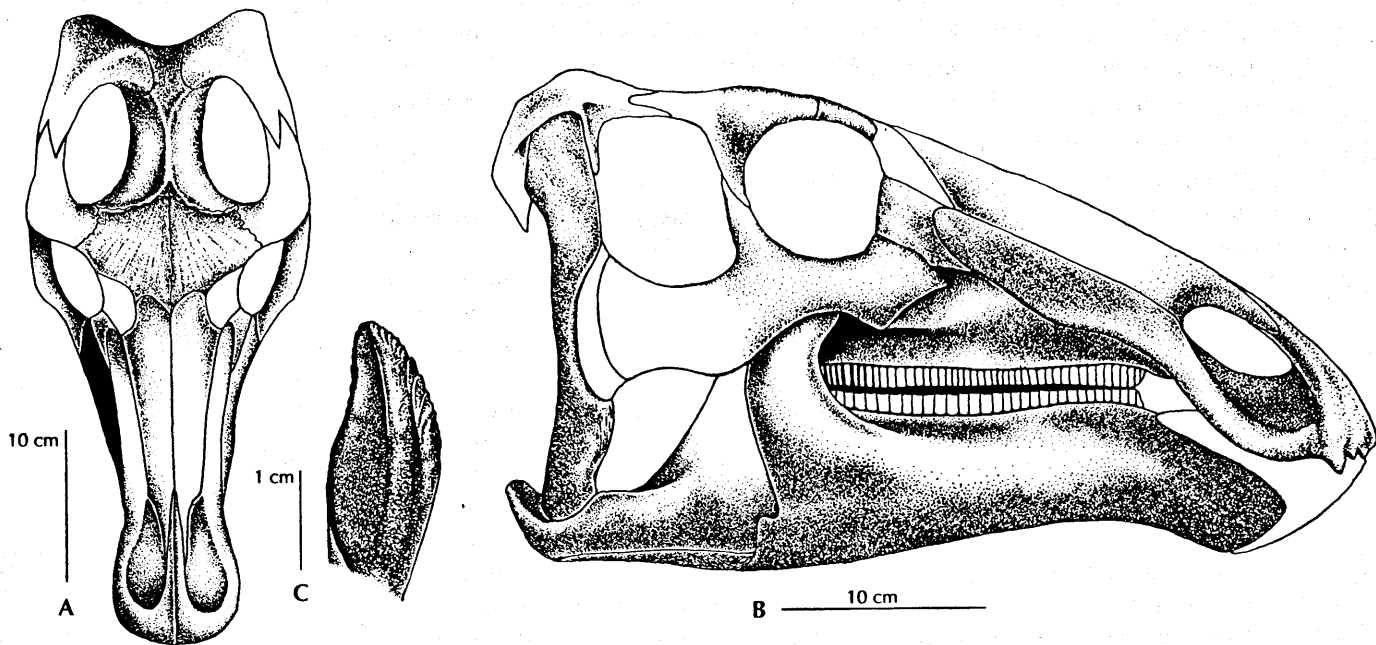


Figure 7. Correlation of the Sînpetru Formation (A) and the Densuș-Ciula Formation (B). ?KT: problematic Cretaceous-Tertiary boundary.



**Figure 8.**  
*Telmatosaurus transsylvanicus.*  
 A, B. Reconstructed skull in right lateral and dorsal views (unstippled regions not preserved and reconstructed after *Gryposaurus notabilis* and *Iguanodon atherfieldensis*). C. Dentary tooth in lingual view (FGGUB [5]).

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upper part of the lower member of the Densuş–Ciula Formation may correlate with those of the top of the Sînpetru Formation farther to the southeast in the basin (Figure 7).

The upper member represents an extension of alluvial fan deposition following the end of volcanic activity in the region. The proximal fan deposits consist of massive, structureless, poorly bedded, and poorly sorted conglomerates. These units merge distally into braided river deposits with coarser, channeled, cross-bedded units and finer overbank deposits. The overbank deposits include fragmentary plant fossils, gastropods much like those found in the Sînpetru Formation, vertical invertebrate burrows, and caliches indicative of arid soil formation.

Vertebrate fossil material from the Densuş–Ciula Formation comes almost exclusively from the silty overbank deposits near the village of Valioara. Elsewhere within the basin, specimens become more fragmentary and rare. Like most of the skeletal material from the Sînpetru Formation, that from the Densuş–Ciula Formation tends to be disarticulated and dissociated. The dinosaur egg nests recently discovered near Tuştea come from the overbank deposits of the Densuş–Ciula Formation.

## Vertebrates from the Haţeg Basin

Since Nopcsa's day, the Haţeg fauna has been largely ignored and its importance for higher-level phylogenies and for paleoecologic and biogeographic analyses underutilized. At the conclusion of Nopcsa's work, the fauna included a handful of dinosaurs (*Telmatosaurus transsylvanicus*, *Rhabdodon priscus*, "*Struthiosaurus*" *transilvanicus*, *Magyarosaurus dacus*, *Megalosaurus hungaricus*), a crocodile (*Allodaposuchus precendens*), a turtle (*Kallokibotion bajazidi*), and a pterosaur (now missing). Over the past decade, considerable material has been added to many of these early-named taxa and new taxa have been added—acipenseriform and characid fishes, amphibians, large and small theropods (including *Bradycneme draculae*, *Heptasteornis andrewsi*, *Elopteryx nopcsai*, and new coelurosauri-

BMNH—BRITISH MUSEUM (NATURAL HISTORY), LONDON, ENGLAND

FGGUB—FACULTATEA DE GEOLOGIE SI GEOFISCA, UNIVERSITATEA BUCURESTI, BUCHAREST, ROMANIA

MAFI—MAGYAR ALLAMI FOLDTANI INTÉZET, BUDAPEST, HUNGARY

MJH—MUZEUL JUDETEAN HUNEDOARA, DEVA, ROMANIA

MNH—MUSEE NATIONAL D'HISTOIRE NATURELLE, PARIS, FRANCE

an material), and a multituberculate mammal (*Paracimexomys? dacicus*). Here we focus on several of the dinosaurs of Transylvania, including *Telmatosaurus transsylvanicus*, *Rhabdodon priscus*, and "*Struthiosaurus*" *transilvanicus*. In addition, we present information on new saurischian material and a dinosaur nesting site from the Hățeg Basin.

#### TELMATOSAURUS TRANSSYLVANICUS

The first fossil vertebrate taxon described from the Hățeg Basin was a new genus and species of hadrosaurid dinosaur that Nopcsa<sup>45</sup> named *Limnosaurus transsylvanicus* (*Limnosaurus* being preoccupied, Nopcsa<sup>48</sup> later renamed the hadrosaurid *Telmatosaurus*). *T. transsylvanicus* remains among the best known taxa from Transylvania. Virtually the entire skull and the majority of the postcranial skeleton are known from a number of individuals of various body sizes.

At ~5 m long and 500 kg, *T. transsylvanicus* was one of the smallest hadrosaurid dinosaurs. Such a body weight is ~10% of average hadrosaurids elsewhere from roughly the same time interval. Fusion of the braincase and vertebral sutures indicates that these individuals were probably fully adult at the time of their death.

**SKULL.** The skull of *T. transsylvanicus* (Figure 8) is known from considerable isolated material and a relatively complete, but crushed specimen (the holotype, BMNH R3386). Upon reconstruction the skull proves to be long, much like *Camptosaurus dispar*, species of *Iguanodon*, *Ouranosaurus nigeriensis*, and other hadrosaurids. The premaxilla is narrow (BMNH R3386, R3842, R4911; FGGUB 1008, 1015). In this feature, it is like *Camptosaurus dispar* and species of *Iguanodon*.<sup>22,56,58,75</sup> The oral margin of the premaxilla is strongly serrate, again much like that in *Iguanodon atherfieldensis*, *I. bernissartensis*, *I. lakotaensis*, and *Ouranosaurus nigeriensis*.<sup>56,58,70,75</sup> The external nares are relatively small, forwardly placed in the rostrum, and do not appear to be surrounded by a circumnarial depression. The caudolateral process of the premaxilla overrides the lateral surface of the lacrimal (BMNH R3386). The remainder of the lacrimal is unknown. The nasal does not seem to be dorsally arched, but slopes gently upward to form the dorsal margin of the muzzle (BMNH R3386; see also MNHN FMR 12, a *Telmatosaurus* specimen from the Upper Cretaceous of southern France).

The frontal of *T. transsylvanicus* (BMNH R3386, R3828, R4911, R4915) is a flat, triangular element. A deep excavation on its dorsal surface receives the caudal portion of the prefrontal. Where it articulates with the parietal, the frontal is raised into a modest transverse ridge. Little can be said about the postorbital except that it makes a complex interdigitate joint with the lateral margin of the frontal; the remainder of the bone is not known. The parietal (known only in BMNH R3386) is long, suggesting that the adductor chamber was somewhat more expansive than in other hadrosaurids. The midline of the parietal is pulled up into a sagittal crest. Within the occiput (based on BMNH R3386, R3387, R3401), the supraoccipital bears lateral facets, each of which articulates with the medial process of the squamosal (the latter process, however, is not known). Articulation between the basioccipital and the atlas is supplemented by well-developed exoccipital condyloids immediately dorsolateral to the occipital condyle. The basal tubera are large.

The squamosal is known from its central body, where it forms a deep cotylus for reception of the head of the quadrate (BMNH R3386). The base of the prequadrate process is preserved where it borders the scar for the adductor mandibulae externus superficialis muscle. Likewise, only the base of the paroccipital process has been recovered. In contrast, the quadrate is known from several specimens (FGGUB 1005, 1006; BMNH R3386, R4911). The shaft is straight. The caudal aspect of the quadrate head is buttressed against the paroccipital process. The cranial margin of the shaft is excavated for reception of the quadratojugal. Directly beneath this excavation, there is a slight buttress, similar to that found in the hadrosaurid *Gilmorecsaurus mongoliensis*. The transversely broad

ORNITHISCHIA  
ORNITHOPODA  
HADROSAURIDAE

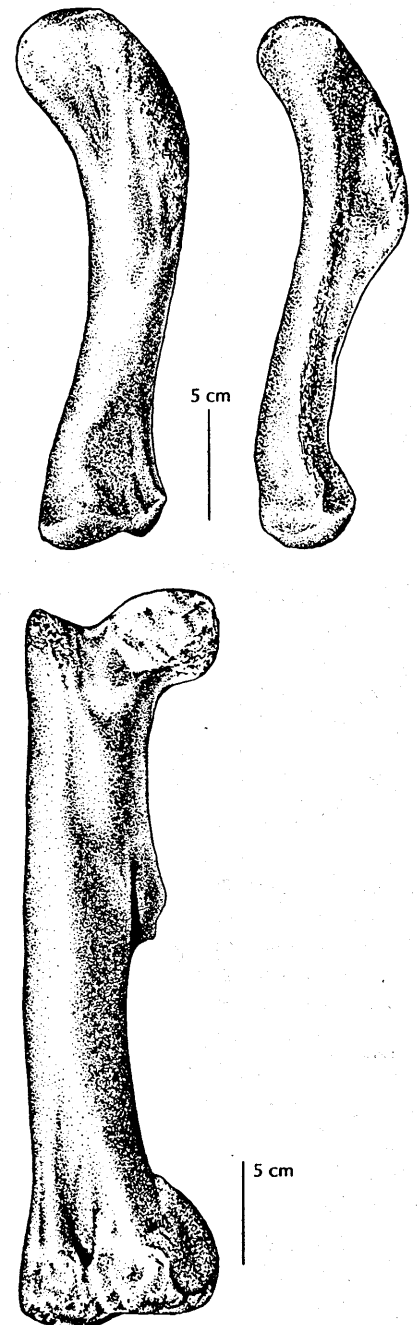


Figure 9. *Telmatosaurus transsylvanicus*. Upper, Cranial and medial views of left humerus (MAFI Ob.3126). Lower, Cranial views of right femur (MAFI v.10338).

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**This manuscript discusses the evolutionarily important Late Cretaceous fauna from the Transylvanian region of Romania. Dominated by dinosaurs, the assemblage provides an important geographic link with the better known dinosaur faunas of North America and Asia. Perhaps more significantly, it contributes a significant perspective on island biogeography using data from the fossil record.**

CORRESPONDENCE

mandibular condyle of the quadrate differs from the more rounded and narrow condition found in virtually all other hadrosaurids.

The rostral portion of the jugal (BMNH R3386, R4911, R11545) forms an isosceles-like triangular articulation with the maxilla. The caudal portion of the jugal is unknown. The maxilla (FGGUB 1010; MAFI Ob.3108, Ob.3109; BMNH R3386, R3388, R4911, R5164) is long and bears a low dorsal process. There is no indication of a laterally-placed antorbital fenestra and fossa. The maxilla contains ~30 tooth positions, compared with 19 to 29 in more primitive iguanodontians (*Iguanodon lakotaensis*, *I. bernissartensis*, *Ouranosaurus nigeriensis*) and 20 to 53 in other hadrosaurids (*Bactrosaurus johnsoni*, *Edmontosaurus regalis*).

The dentary is known from a number of specimens of *T. transsylvanicus* (MAFI Ob.1943; BMNH R2967, R3386, R3401). In the region of articulation with the prementary, the rostral end of the dentary bends ventrally and medially to form the mandibular symphysis. There is only a modest diastema between the prementary (estimated from the prementary articular surface on the dentary) and the first dentary tooth. The largest dentary of *T. transsylvanicus* (BMNH R3396) contains ~30 tooth positions, comparable to *Bactrosaurus johnsoni*.<sup>73,76,77</sup> The large surangular (BMNH R3386, R4911; MAFI Ob.3123, v.13497) forms the caudal part of the coronoid process, the mandibular glenoid, and a portion of the retroarticular process. The glenoid is a shallow, cup-shaped depression. A prominent lateral lip forms the lateral margin of the glenoid. Only the base of the retroarticular process of the surangular is preserved in existing specimens of *T. transsylvanicus*. There is no surangular foramen.

Of the palate, the pterygoids are preserved only in BMNH R3386, but these are extremely crushed. Other palatal elements are not known.

**DENTITION.** Both maxillary and dentary dentitions are organized into dental batteries. Maxillary batteries consist of usually one, but sometimes two, functional teeth and as many as three replacement teeth per tooth family. This organization compares with two to three functional teeth and an estimated four or five replacement teeth per tooth position in the dentary. Maxillary teeth are high and relatively narrow (mean tooth width = 0.4 cm; e.g., MAFI v.13508). As in all "higher" ornithopods, it is the buccal face of the tooth that is enameled. Centrally, there is a strong median carina, but no secondary ridges. The margins of the crown are highly denticulate, but the denticles are not supported by marginal ridges on the buccal face. By contrast, teeth within the dentary are wider than maxillary teeth and relatively wider than dentary teeth in other hadrosaurids (mean tooth width = 0.8 cm; e.g., FGGUB [5]). The lingual surface of the crown bears only a shallow primary ridge and sometimes a modest secondary ridge. The mesial and distal margins of the crown are denticulate; each denticle is supported by ridges on the enameled lingual face of the crown.

**VERTEBRAE.** The vertebral column is poorly known in *T. transsylvanicus*. The best of this material includes portions of the cervical series and two partial sacra (BMNH R3841, R4911) that Nopcsa<sup>53</sup> referred to this species. Additional isolated vertebral material is also known (BMNH R3809, R3842, R4915, R4973). The axis bears a prominent, conical dens that extends from the well-buttressed cranial surface of the axial centrum. The neural spine is long, arched, and blade-like. The next three cervicals are strongly opisthocoelous. A sagittal ridge on the ventral surfaces of these vertebrae is most accentuated on the undersurface of the fifth cervical. Laterally positioned ridges run parallel to the sagittal ridge. The pre- and postzygapophyses are much like those in other hadrosaurids.

The number of dorsal vertebrae is unknown in *T. transsylvanicus*. Isolated dorsals indicate that the centra are slightly opisthocoelous cranially to virtually platycoelous caudally within the series. The neural spines are of modest size, comparable to those in some other hadrosaurids (*Gryposaurus notabilis*, *Edmontosaurus regalis*). Partial sacra referred to *T. transsylvanicus* indicate that the sacrum was composed of at least four vertebrae; more were almost certainly present. The ven-

tral surface of these sacrals bears a strongly developed longitudinal ridge. The number of caudals is also unknown in *T. transsylvanicus*, but probably ranged to >50. Proximal members of this series bear modest neural spines, much like those of *Gryposaurus notabilis* and species of *Iguanodon*.

**LIMBS.** The appendicular skeleton is partially known in *T. transsylvanicus* (Figure 9). The scapula (FGGUB [4]) is relatively long and narrow. The blade is slightly expanded and an acromial process is modestly developed forward of the glenoid region. A single fragmentary coracoid (BMNH R3843) preserves the glenoid facet and a large coracoid foramen adjacent to the scapular junction. The humerus (MAFI Ob.3126; BMNH R3842, R3845, R3847) is somewhat gracile. It bears a rounded deltopectoral crest that extends only a short distance from the shaft, similar to the condition found in *Camptosaurus dispar*, species of *Iguanodon*, and *Ouranosaurus nigeriensis*. The cranial margin of the deltopectoral process is not reflected medially like that in hypsilophodontids. The radial condyle is somewhat narrow, while the ulnar condyle is much larger and teardrop-shaped. The ulna (MAFI Ob.3124, Ob.4212; FGGUB 1078) is long and narrow. The proximal head is formed into a triangular articular surface for the humerus. The radius and manus are not known.

Of the hindlimb, only the femur and tibia are known for *T. transsylvanicus* from the Hațeg Basin (an ischium from northeastern Spain, however, has been referred to *Telmatosaurus* by W. Brinkmann<sup>5</sup>). The femur (MJH 66; MAFI Ob.3128, v.10338; BMNH R3846, R4914, R11539) has a slightly laterally bowed shaft. The greater and lesser trochanters are separated by a modest vertical cleft. The well-developed fourth trochanter crosses the caudomedial aspect of the shaft. The femoral condyles are large, face slightly medially, and meet cranially to form an extensor "tunnel" for the insertion tendon of the iliotibial muscles. The tibia (BMNH R3845) is relatively straight and typically twisted about its long axis.

**DISCUSSION.** Hadrosauridae comprises nearly 25 genera and 40 species, mostly from the western interior of North America, but also from central and eastern Asia. *T. transsylvanicus* shares with these forms a common *Bauplan*, including a dental battery consisting of three to five closely packed replacement teeth per tooth position, loss of the surangular foramen, and mesiodistal narrowing of the maxillary teeth, among other features.<sup>77</sup>

Within Hadrosauridae, the majority of species can be allotted to two major subgroupings, the well-known lambeosaurines and the hadrosaurines.<sup>77</sup> However, several taxa are positioned below the clade that includes lambeosaurines and hadrosaurines. Basally among these is *T. transsylvanicus*, which lacks the following features found in more derived hadrosaurids: narrowing of dentary teeth; development of strong median carina on dentary teeth; narrowing of the mandibular condyle of the quadrate; absence of the strongly serrate oral margin of the premaxilla; and presence of a strong, angular deltopectoral crest on the humerus. On the basis of such a character distribution, *Telmatosaurus transsylvanicus* can be placed at the most primitive level within the hadrosaurid clade.

### RHABDODON PRISCUS

What is currently known about the ornithischian dinosaur *Rhabdodon priscus* (Figure 11) comes primarily from early literature.<sup>46,47,49,52,53</sup> Nopcsa<sup>44</sup> originally noted the existence of this taxon as *Mochlodon*, an ornithopod genus established by H. G. Seeley<sup>67</sup> from the Gosau Beds of Austria. Following his preliminary note, Nopcsa<sup>45,47,49</sup> compared his Transylvanian material with other ornithopods from Europe and with those from North America (specifically *Camptosaurus*) before observing<sup>50</sup> that *Mochlodon* was similar to a genus from southern France named *Rhabdodon*.<sup>39</sup> Retaining the name *Mochlodon* for the Hațeg material, Nopcsa also referred it to Camptosauridae. Much later, A. S. Romer<sup>64,65</sup> transferred it, plus all

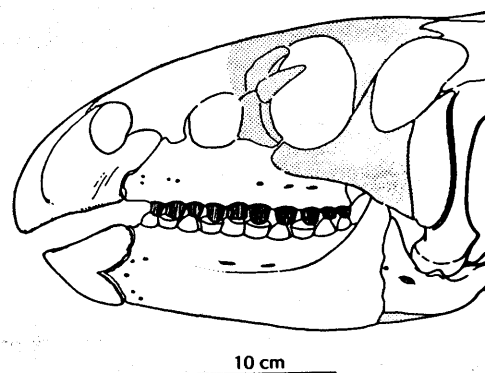
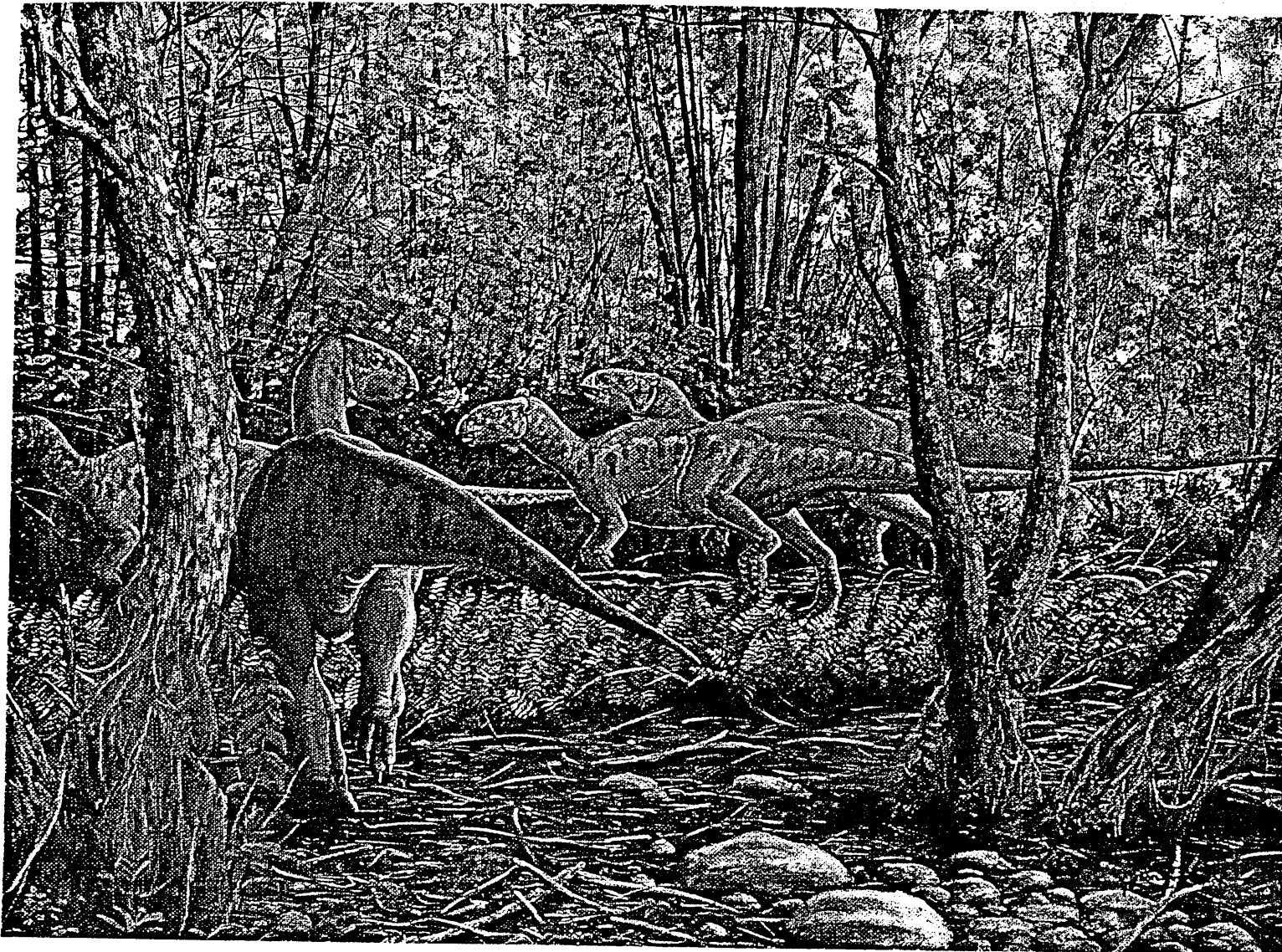


Figure 10.  
*Rhabdodon priscus*. Left lateral view of the skull. Stippled areas are those for which there is no good information.

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ORNITHISCHIA  
ORNITHOPODA  
EUORNITHOPODA  
SEDIS MUTABILIS



**Figure 11.**  
*Rhabdodon priscus.*  
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members of Camptosauridae, to Iguanodontidae. Not until 1986 was the validity of the name *Rhabdodon* over *Mochlodon* finally established.<sup>6</sup> The systematic position of *R. priscus* was called into question throughout the 1980s, with suggestions that it belonged in Hypsilophodontidae.<sup>57,73,79</sup> P. C. Sereno<sup>68</sup> commented that this animal is probably a very primitive iguanodontian (i.e., the clade of *Iguanodon* and hadrosaurids, among others). Perhaps on these grounds, R. L. Carroll<sup>13</sup> retained *Rhabdodon* as an iguanodontid. More recently, W. Brinkmann<sup>7</sup> supported hypsilophodontid affinities of this taxon. Finally, D. B. Norman and D. B. Weishampel<sup>59</sup> placed *R. priscus* as a possible iguanodontian (*sensu* Sereno<sup>68</sup>), but without comment and prior to the analyses presented here.

**SKULL.** The skull of *Rhabdodon priscus* is known only from isolated, yet well-preserved specimens. Of these, BMNH R3389, R3393, R3395, R3396, R3398, and R3402 are commensurate in size and of exactly the same quality of preservation; we strongly suspect that they belong to a single dissociated skull. Consequently, we have produced the first reconstruction ever attempted of the skull from this and other material (BMNH R3393, R3394, R3395, R3396, R3398, R3402, R3411, R4901, R4916, R5491) (Figure 10).

The skull is relatively large but compact, with a short facial region. The premaxilla is toothless, narrow, and unexpanded along the oral margin. Hence the beak is narrow and nearly pointed in lateral view. There is no evidence of serra-

tions along the oral margin. The dorsal process forms a slender wedge that fits medially against the rostral process of the nasal above the external naris. This rostral process is also embayed to form the caudal margin of the external naris. The dorsal process of the nasal appears to be relatively short, and the ventral process is rostrocaudally expanded where it meets both the lateral portion of the premaxilla and the dorsal part of the maxilla.

The maxilla is robust and contains at least 10 tooth positions. The rostral tip of the maxilla is prolonged as a blunt, finger-shaped process fitting into a median recess formed between the two premaxillae. The external wall of the maxilla overlaps the caudolateral process of the premaxilla and the lower margin of the nasal. Immediately behind the maxilla-nasal suture, the lateral wall of the maxilla is interrupted by the large antorbital fenestra. The caudal margin of this fenestra was probably formed by both the maxilla and lacrimal, but this portion of the skull is not preserved. The maxilla is transversely thickened above the tooth row, producing a noticeable overhang that mirrors a similar lateral thickening of the mandible. The effect of such thickenings is the characteristic cheek recesses seen in ornithischian dinosaurs. The bones surrounding the orbit and temporal openings are mostly missing, so the morphology indicated in Figure 10 is hypothetical.

The squamosal in *R. priscus* is well-preserved and has a long medial process contacting the parietal and a thin, but broad rostral process contacting the postorbital. Ventrally, the body of the squamosal bears a cup-shaped cotylus for the head of the quadrate. Adjacent to the cotylus, the prequadratic and paroccipital processes limited movement of the quadrate head. The quadrate is unusually massive, with a thick shaft marked by a large, complex lateral excavation running almost the length of the lateral surface of the bone. This surface served as the sutural contact for the quadratojugal. Although the latter bone has not been identified, it clearly was very large.

The lower jaw is very stout in *R. priscus*. The predentary is robust with a smooth occlusal margin. The ventral process is divided as it covers the undersurface of the mandibular symphysis. The lateral processes enclose the front of the dentary by way of a strong overlapping suture. The dentary is large and robust, housing 10 tooth positions. The dorsal and ventral margins are subparallel. Caudally, there is a prominent, but slender coronoid process formed by the predentary and surangular. The surangular has two foramina. The smaller lies close to the surangular-dentary suture and may represent the homologue of external mandibular fenestra of other archosaurs, whereas the larger is found in the lateral wall of the surangular immediately rostral to the glenoid. In addition, the lateral margin of the glenoid is marked by a knoblike process whose prominence is peculiar to *R. priscus*. The part of the retroarticular process formed by the surangular is elongate, but not upturned.

**DENTITION.** The dentition of *R. priscus* is distinctive. Maxillary teeth are approximately equidimensional in buccal view. Numerous subequal, vertically oriented ridges adorn the enameled buccal surface. Each ridge culminates in a denticle along the margin of the crown. Although the dentary dentition is much like that of the maxilla, these lower teeth differ in having a strong primary ridge arising from the middle of the enameled lingual surface. Both maxillary and dentary teeth have a slight cingulum at the base of the crown.

**LIMBS.** The remainder of the skeleton of *R. priscus* is well-preserved and indicates a 3- to 4-m-long ornithopod of somewhat robust build. The humerus (FGGUB 1013; MAFI Ob.3077, Ob.3078; BMNH R3809, R3810, R3814) is of moderate length and construction. The deltopectoral crest is angular and slightly medially deflected at its tip, much like the condition seen in *Hypsilophodon foxii* and *Orodromeus makelai*. The distal condyles are subequal in size. The ulnar condyle is slightly depressed below the level of the radial condyle. The ilium is unique among ornithopods in having a long, twisted cranial process and a somewhat

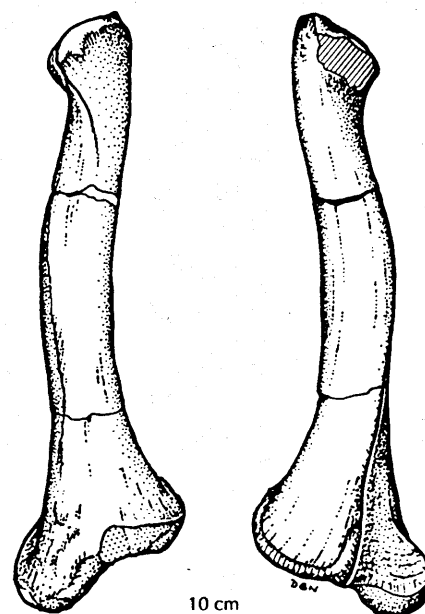


Figure 12.  
*Rhabdodon priscus* right tibia: left,  
anterior; right, posterior.

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This is a refreshing and important paper on dinosaurian paleobiology. It represents a major contribution in that it is a modern review of a "forgotten" fauna, and outlines the extremely interesting scenario of relict forms living on a Cretaceous archipelago extending between more highly evolved continental faunas of the remainder of both the northern and southern hemispheres.

A REVIEWER

ORNITHISCHIA  
ANKYLOSAURIA  
NODOSAURIDAE

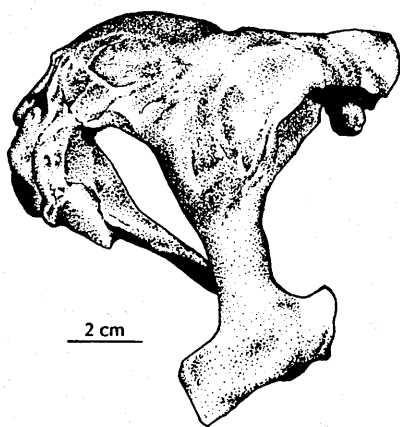


Figure 13.  
"Struthiosaurus" transilvanicus. Right lateral views of the skull (BMNH R4966).  
DAVID B. WEISHAMPEL

truncated caudal process (FGGUB [25]; BMNH R3810, RR3813). The region above the acetabulum is deep. The ischium (BMNH R3810, R3814, R4900; MJH 77) is long and ventrally curved and lacks an obturator process. The pubis is unknown. The femur (BMNH R3810, R3811, R3813, R3814, R3816, R4900) is moderately curved along its long axis. The cranial portion of the femoral condyles is less expanded in *R. priscus* than in *T. transylvanicus*. The tibia is approximately as long as the femur, but robustly constructed and somewhat bowed (FGGUB [8]) (Figure 12).

DISCUSSION. The only possibilities for the position of *R. priscus* among higher ornithopod taxa include a relationship within Hypsilophodontidae or as a member of the iguanodontian plexus prior to the evolution of hadrosaurids. Of the synapomorphies of Hypsilophodontidae and Iguanodontia that bear on existing material of *R. priscus*, two appear to ally *R. priscus* with Iguanodontia (parallel dentary margins, absence of premaxillary teeth). However, another two (ridges confluent with the marginal denticles on maxillary and dentary teeth, cingulum at the base of maxillary and dentary crowns) suggest a hypsilophodontid relationship. Clearly, the affinities of *R. priscus* are problematic and will require a more complete treatment of the broad-based relationships of Euornithopoda (i.e., Hypsilophodontidae + Iguanodontia).

### "STRUTHIOSAURUS" TRANSILVANICUS

In 1871, E. Bunzel<sup>11</sup> erected the name *Struthiosaurus austriacus* for material (a small, isolated basicranial fragment) from the Gosau Beds of Niederösterreich, Austria, thought to be ankylosaurian. Nopcsa's<sup>51,55</sup> study of the ankylosaur material from the Hațeg Basin involved close comparisons with *S. austriacus* and other ankylosaur taxa from Europe. On the basis of these studies, Nopcsa referred his material to Bunzel's *Struthiosaurus* as *S. transylvanicus*. W. P. Coombs and T. Maryańska<sup>18</sup> consider *S. austriacus* as a *nomen dubium*. Consequently, the Hațeg ankylosaur, though regarded as generically and specifically distinct, stands without a proper name. Following Coombs and Maryańska,<sup>18</sup> we place the name in quotes to indicate that "Struthiosaurus" still lacks a generic identity.

Originally collected nearly 70 years ago, "*S.*" *transilvanicus* consists of a variety of skull material (braincase, skull roof, temporal region) (Figure 13), as well as vertebrae, scapulocoracoid, and dermal armor (BMNH R4966). Specimens are small, but probably adult. The skull of "*S.*" *transilvanicus* is distinctive among ankylosaurs in having closed supratemporal fenestrae, narrow infratemporal fenestrae, and fusion of the paroccipital process and squamosal. Other aspects of the anatomy of this animal enable the determination of its relationship with other known ankylosaurs (features taken from Coombs and Maryańska<sup>18</sup>). First, "*S.*" *transilvanicus* is clearly a nodosaurid, the longer-lived of the two ankylosaur families. This allocation is based on a variety of cranial and postcranial characters. The cranial features are concentrated in the floor of the braincase and along the skull roof. The basiptyergoid processes are rounded, rugose, and stublike. The occipital condyle, composed only of the basioccipital, is hemispheric and separated from the remainder of the braincase by a short neck. This basioccipital complex is angled downward from the long axis of the skull by ~50°. Features within the skull roof include a large plate between the orbits and a rostrocaudally narrow plate along the caudal edge of the skull. In addition, there are three scutes above the orbits and several small scutes rostral to the orbits. Postcranially, the scapular spine is displaced caudoventrally toward the glenoid. The coracoid is large and long relative to its dorsoventral width. Finally, the ischium is ventrally flexed near its midlength.

DISCUSSION. Within the nodosaurid clade, "*S.*" *transilvanicus* shares a number of postcranial features with more derived taxa, including *Sauropelta edwardsi*, *Panoplosaurus mirus*, and species of *Edmontonia*. For example, the scapular spine is knoblike and angled caudoventrally to form a distinct prespinous fossa.

The dermal spines are also typical of these derived nodosaurids. However, "*S.*" *transilvanicus* lacks the fusion of the scapula with the coracoid, typical of the more derived nodosaurid taxa. Although this condition may be because of the immaturity of existing material, W. P. Coombs and T. Maryńska<sup>18</sup> document similar conditions in fully adult members of other nodosaurid taxa. "*S.*" *transilvanicus* may also have possessed premaxillary teeth,<sup>50,54</sup> much like those of *Sauropelta edwardsi* and *Silvisaurus condrayi*. As a consequence of the distribution of these features, "*S.*" *transilvanicus* assumes a primitive position in nodosaurid phylogeny.<sup>18</sup>

## SAURISCHIAN DINOSAURS

Until recently, theropod material from the Late Cretaceous of Europe has consisted of isolated teeth, vertebrae, femora, and tibiotarsi, many of them poorly preserved. As a consequence, virtually all of these theropods (*Megalosaurus lonzeensis*, *M. bredai*, *M. pannoniensis*, *M. hungaricus*) are inadequate for taxonomic assignment.<sup>42</sup> Of the theropod material collected from the Hateg Basin, virtually all appears to be non-diagnostic at least at the generic level. Some (*Bradycneme draculae*, *Heptasteornis andrewsi*, *Elopteryx nopcsai*) were originally regarded as avian, but now appear to be possible troodontids.<sup>60</sup> Most of this material, however, can only be attributed to Theropoda indet.

**THEROPODA.** Recent collections by the Universitatea Bucuresti have partially changed this impoverished situation. This material, consisting of the caudal portion of a large skull, represents the most complete theropod material from the Hateg Basin (FGGUB 1083). From an anatomical and systematic point of view, the best parts of this new material include the occiput and suspensorium (Figure 14). The supraoccipital portion of the occiput is elevated, much like that of *Allosaurus fragilis*. There is only a faint expression of a vertical ridge on the caudal face of the supraoccipital. The bases of the paroccipital processes are extremely robust, but it is unknown whether the distal portions are pendent (as in *A. fragilis*) or straight (cf. tyrannosaurids such as *Alioramus remotus* and *Tyrannosaurus rex*). The basal tubera project ventrally from the basisphenoid as a broad, vertical apron. The quadrate consists of the shaft, mandibular condyle, and articulation with the quadratojugal (also partially preserved). Missing are the pterygoid process and dorsal head. The paraquadratic foramen appears to be relatively large. The lateral portion of the mandibular condyle is expanded over the medial region, giving a medially elevated rotational axis to the jaw joint. A small bony fragment abutting the upper portion of the quadrate shaft may prove to be a part of the prequadratic process of the squamosal.

Given the distribution of available characters (among them, lack of a prominent supraoccipital crest, enlarged lateral region of the mandibular condyle), this new theropod appears not to be an abelisaur, as has been suggested for a newly described theropod specimen from southern France.<sup>9</sup> Whether it proves to be a tyrannosaurid or other member of Carnosauria remains to be seen.

**SAUROPODA.** In addition to the new theropod material, the Universitatea Bucuresti field party has collected a small sauropod braincase and a skull roof (FGGUB 1007) from the Pui locality. The braincase (Figure 15) is short and extremely deep, with depressed basal tubera and basiptyergoid processes. The basal tubera and basiptyergoid processes abut one another to form the most ventral portions of the depressed basisphenoid. Lack of fusion between the floor (basioccipital, basisphenoid, presphenoid) and the walls (exoccipital, opisthotic, prootic, laterosphenoid, orbitosphenoid) indicate the immaturity of this specimen. Virtually all of the cranial nerve and vascular foramina are well preserved on both sides of the braincase. The parietals are separated from one another by a sagittal suture, probably indicating extreme immaturity of the individual. These elements are relatively wide and short, making a broad, transverse contact with the frontals. Laterally on the parietals near the parietofrontal articulation are short, ovate

## SAURISCHIA

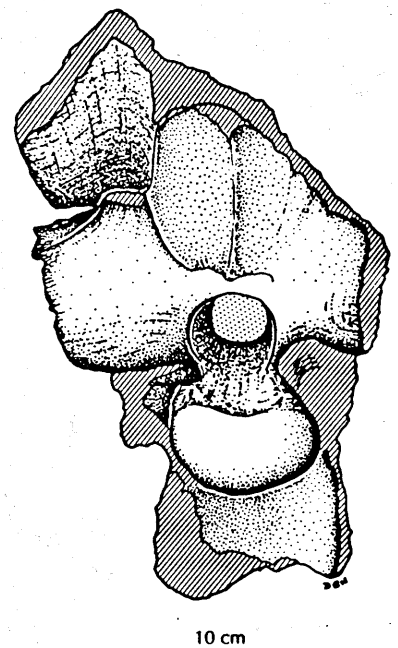


Figure 14.  
Occipital view of the new theropod material from the Hateg Basin (FGGUB 1083).  
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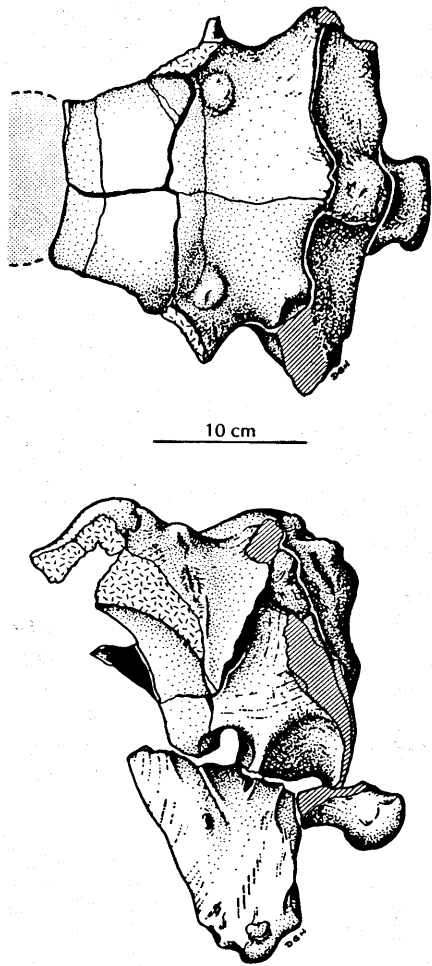


Figure 15.  
 Juvenile titanosaurid braincase (FGGUB  
 1007). A,B. Left lateral and occipital view.  
 DAVID B. NORMAN

excrescences, somewhat like the pedicels of cervid antlers. The frontal makes a transverse joint with the nasal. The latter is relatively short, indicating that the external naris has assumed a caudodorsal position.

Sauropods are reasonably well known from the Hațeg Basin, but they consist entirely of isolated postcranial material, most of which is relatively small but presumed to be adult. None of these specimens has ever been properly described, but nonetheless has been referred to *Titanosaurus dacus*.<sup>50</sup> This species was later transferred to *Magyarosaurus* by F. von Huene,<sup>32</sup> a taxonomic assignment currently accepted by J. S. McIntosh.<sup>40</sup>

#### DINOSAUR EGG NESTS

In 1989, the Universitatea Bucuresti discovered a nesting horizon near the village of Valioara,<sup>27</sup> the first from Hațeg Basin. On a single bedding plane, 14 eggs are arranged in four linear clutches; each clutch contains either two or four eggs. The distance between clutches is ~0.5 m. Although variously deformed, the eggs would have been subspherical and ~150 mm in diameter (Figure 16). The eggshell is ~2.4 mm thick and the external surface displays a highly irregular tuberculated (tubocanaliculate) pattern. The size, shape, and texture of these eggs are similar to those from southern France, although the latter were laid out in sweeping curves.<sup>4,33</sup> These European egg specimens often differ from those elsewhere in the world: most of the eggs from the Mongolian People's Republic, the People's Republic of China, the United States, and Canada are oval or oblong and range from 120 to 170 mm in length.<sup>23,30,31,81</sup> Surface texture varies from striated to irregularly tuberculated.<sup>29,30</sup>

We earlier suggested that these eggs may have been laid by the sauropod *Magyarosaurus*.<sup>27</sup> However, we now have embryonic remains that are associated with these egg clutches. Because embryonic material clearly pertains to Hadrosauridae, the most likely candidate among the Hațeg fauna to have laid the eggs is *Telmatosaurus transsylvanicus*.

#### Discussion—Dispersal or Vicariance?

Most studies of the evolution of island faunas have focused on the short-term ecological aspects of the evolutionary relationships among organisms. In contrast, our work on insular evolution involves the long-term perspective that derives from the fossil record. In doing so, we are pursuing the relationships among systematics, paleoecology, geology, and geochronology in island evolution based principally on the Upper Cretaceous Hațeg Basin sites of the Transylvania region of western Romania and elsewhere in Europe.

Such broad geographic distributions could be explained by dispersal or vicariance. Dispersal involves the movement of organisms across existing barriers to determine subsequent distribution. Vicariance entails the formation of barriers after the taxa have established their early biogeographic ranges. Subsequent distributions thus represent the fragmentation of once more-continuously distributed taxa.

Nopcsa<sup>51,55</sup> was the first to use dispersal models to explain the distribution of the Hațeg assemblage relative to other Late Cretaceous faunas. He suggested that the primitive nature of many of the Transylvanian taxa was the direct result of island hopping early in the history of each clade. For example, the primitive position of *T. transsylvanicus* among hadrosaurids is at odds with its late Maastrichtian age. In contrast, the oldest member of the sister taxon to *T. transsylvanicus* (lambeosaurines + hadrosaurines) is at least middle Campanian if not older.<sup>74</sup> This minimal divergence time

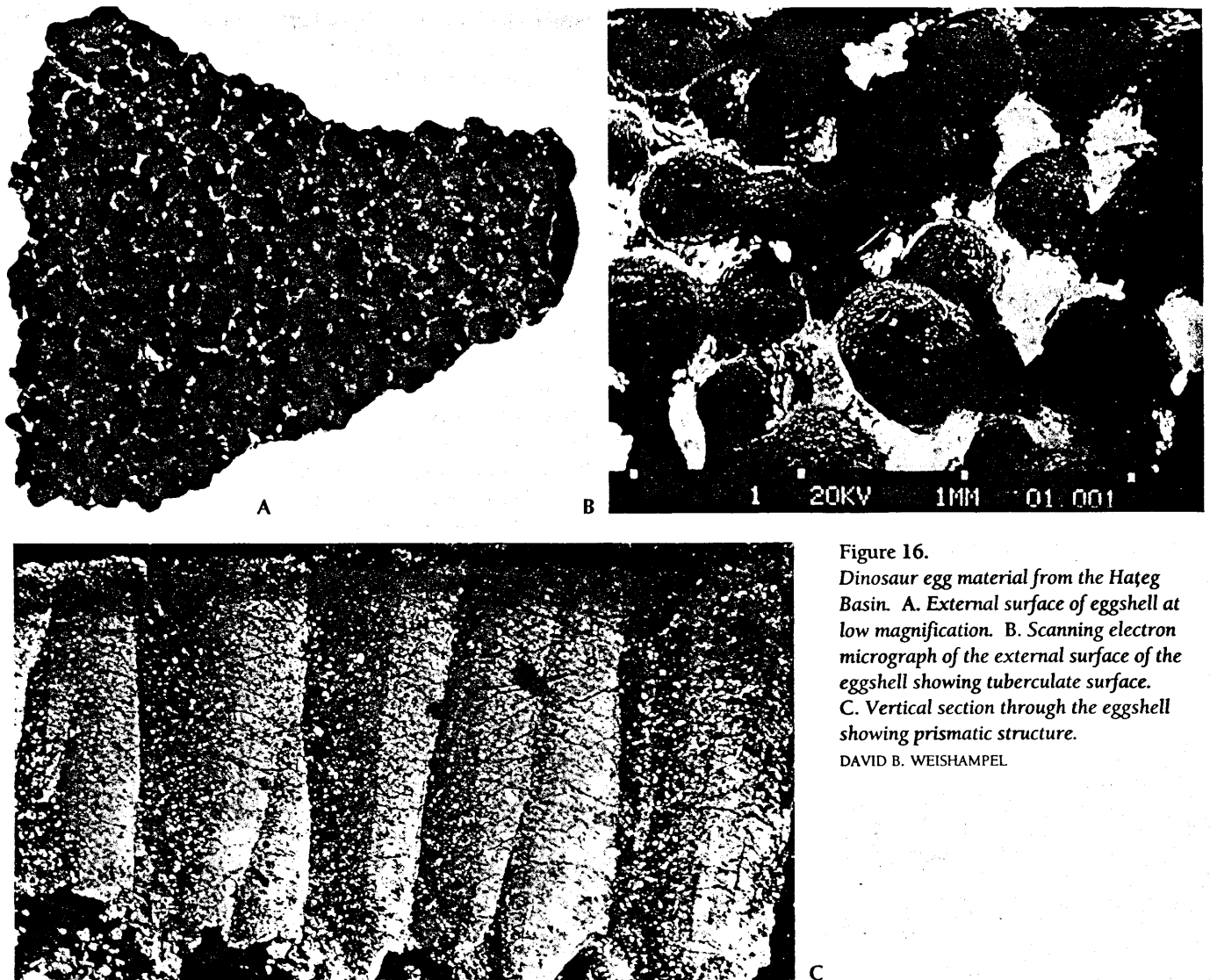


Figure 16.  
Dinosaur egg material from the Hațeg Basin. A. External surface of eggshell at low magnification. B. Scanning electron micrograph of the external surface of the eggshell showing tuberculate surface. C. Vertical section through the eggshell showing prismatic structure.

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between *T. transylvanicus* and its sister taxon implies early island dispersal followed by at least 18 to 20 Ma years of isolation.

"*Struthiosaurus*" *transilvanicus* is a primitive taxon within Nodosauridae, much as *T. transylvanicus* is within Hadrosauridae. The oldest member of its sister taxon, the clade of *Sauropelta edwardsi*, *Silvisaurus condrayi*, *Panoplosaurus mirus*, and species of *Edmontonia*, is late Aptian in age, suggesting that >50 Ma separate "S." *transilvanicus* from these more derived nodosaurids. Such data again imply island hopping early in the history of the nodosaurid clade.

Although Nopcsa appears to have favored dispersal as the chief control on the isolated distribution of Hațeg taxa, a vicariance interpretation involves taxonomic differentiation coincident with the establishment of geographic barriers. Subsequent occurrences then indicate survival in refugia. A vicariance interpretation of the distribution of *T. transylvanicus* begins with evaluating the distribution of "higher" iguanodontians (*Iguanodon*, *Ouranosaurus*, and hadrosaurids, among others). These "higher" iguanodontians occur throughout Europe, northern Africa, and North America. Basally in Hadrosauridae, *T. transylvanicus* is restricted to Europe. Subsequent hadrosaurid distribution is Laurasian (i.e., North



**The small size of the taxa suggests island effects. And the early minimum divergence times of some of the taxa suggests early (?Neocomian) isolation of some of the ancestral lineages. The island was probably colonized at a later date by hadrosaurs.**

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America, and central and eastern Asia) with a meager record in South America.<sup>3</sup> The occurrence of *T. transylvanicus* in Europe suggests the development of barriers that separate this taxon from outgroup iguanodontians sometime prior to the middle Campanian (ca. 78 Ma BP). The North American and Asian distribution of remaining hadrosaurids requires further barrier formation or dispersal.

"S." *transylvanicus* and the majority of other nodosaurids come from Euroamerica, although important material is also known from Australia and Antarctica.<sup>21,42</sup> Of those nodosaurid taxa whose relationships have been analyzed,<sup>18</sup> basal nodosaurids are distributed solely in Europe. It is only with the evolution of *Sauropelta edwardsi* (at least by the Aptian; ca. 115 Ma BP) that the group assumes a North American distribution. The European distribution of "S." *transylvanicus* suggests the development of one or more barriers that separate this species from North American nodosaurids. The progressive opening of the northern part of the North Atlantic would certainly have acted as such a barrier.

A complete phylogeny of nodosaurid taxa has yet to be attempted and the addition of such species as *Minmi paravertebra* from Australia may alter the evolutionary and biogeographic patterns described here. For instance, the relationships of *M. paravertebra* to other nodosaurids might conceivably indicate a Gondwanan alliance for "S." *transylvanicus*, despite what appears to be largely a Euroamerican distribution.

How the remaining Håteg taxa and their systematics affect biogeographic interpretations remains to be seen. For instance, *Rhabdodon priscus* is as yet ambiguous with respect to hypsilophodontid versus iguanodontian relationship. Thus it is not possible to explore the degree to which its distribution in Europe results from vicariance or dispersal. The test of these propositions will depend in large part on the phylogenetic resolution of *R. priscus* within Euornithopoda.

The only members of the Håteg fauna that have an obvious relationship with Gondwana taxa are the titanosaurid sauropods.<sup>40</sup> Virtually all other titanosaurids are distributed across the southern hemisphere, from India in the east, throughout Africa, to South America in the west.<sup>74</sup> At present, the phylogenetic relationships of taxa within Europe, and between Europe and southern continents is unknown.<sup>40</sup> Thus, island dispersal or vicariance refugia as explanations for titanosaurid distribution in Europe and elsewhere remains poorly understood.

The faunas of Europe offer the possibility of establishing the evolutionary interplay among islands within the archipelago. Members of other European faunas bear some relationship to those of the Håteg Basin, but at present, we can say only that a high degree of similarity often occurs among the faunas from Håteg, Gosau, southern France, and Spain.<sup>74</sup> For example, many appear to include material referable to genera from the Håteg fauna: *Telmatosaurus*, *Rhabdodon*, and "Struthiosaurus." Less often, material has been referred to a number of higher taxa (but not to the same species) known from the Håteg fauna, including several nodosaurids, titanosaurids, and theropods. Finally, some taxa (*Hypselosaurus priscus*, *Titanosaurus indicus*, ?abelisaur<sup>9</sup>) known elsewhere in the European archipelago are unknown in the Transylvanian fauna. Within Europe relationships of these taxa will profoundly influence the interpretation of their regional distribution within the archipelago.

What we know about the evolutionary distribution of *Telmatosaurus*

*transylvanicus* and "*Struthiosaurus*" *transilvanicus* does not refute either isolation via dispersal or the imposition of barriers that resulted in European refugia. However, the stratigraphic distribution of sister taxa provides some limits that, when combined with both regional geology and paleogeography, may militate against island refugia and vicariance for the majority of the Mesozoic in Europe. From at least the beginning of the Jurassic, broad expanses of shallow and deep ocean dominated the region; islands were few and relatively far between. Marine barriers that could have altered the distribution of terrestrial vertebrates appear to have been in place well before the appearance of nodosaurids and hadrosaurids (and perhaps remaining members of the Hateg fauna).

Our work on the Hateg fauna comprises a research program much like inquiries into the distribution of recent organisms using evolutionary theory and island biogeography. In contrast, research that centers specifically on insular evolution in the fossil record has been rare. Our research on the Late Cretaceous European archipelago, focused on the Hateg Basin, is an effort to redress this situation. By combining systematics, paleogeography, geology, and paleoecology, the Hateg assemblage and other European faunas provide a unique perspective on long-term aspects of insular evolution at the end of the Mesozoic.

## BIBLIOGRAPHY

1. Anastaiu, N.; & Ciobuca, D.: Non-marine uppermost Cretaceous deposits from Stei-Densus region (Hateg Basin): sketch for a facies model. *Revue Roumaine de Géologie, Géophysique et Géographie, Bucuresti (Géologie)* 33:43-53; 1989.
2. Antonescu, E.; Lupu, D.; & Lupu, M.: Corrélation palynologique du Crétacé terminal du sud-est des Monts Metaliferi et des Dépressions de Hateg et de Rusca Montana. *Anuarulu Institutul Geologie-Geofizica Bucuresti (Stratigrafie si Paleontologie)* 59:71-77; 1983.
3. Bonaparte, J.F.; Franchi, M.R.; Powell, J.E.; & Sepulveda, E.G.: La Formación Los Alamitos (Campaniano-Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* n. sp. (Hadrosauridae). Significado paleogeográfico de los vertebrados. *Asociación Geológica Argentina Revista* 39:284-299; 1984.
4. Breton, G.; Fournier, R.; & Watte, J.-P.: Le lieu de ponte de dinosaures de Rennes-le-Château (Aude). *Annales du Musée du Havre* 32:1-12; 1986.
5. Brinkmann, W.: Erster Nachweis eines Hadrosauriers (Ornithischia) aus dem unteren Garumnium (Maastrichtium) des Beckens von Tremp (Provinz Lerida, Spanien). *Paläontologische Zeitschrift* 58:295-305; 1984.
6. Brinkmann, W.: *Rhabdodon* Matheron, 1869 (Reptilia, Ornithischia): proposed conservation by suppression of *Rhabdodon* Fleischmann, 1831 (Reptilia, Serpentes). *Bulletin of Zoological Nomenclature* 43:269-272; 1986.
7. Brinkmann, W.: Zur Fundgeschichte und Systematik der Ornithopoden (Ornithischia, Reptilia) aus der Oberkreide Europas. *Documenta Naturae* 25:1-157; 1988.
8. Buffetaut, E.; Marandat, B.; & Sigé, B.: Découverte de dents de Deinonychosauriens (Saurischia, Theropoda) dans le Crétacé supérieur du Sud de la France. *Comptes-rendus hebdomadaires des séances de l'Académie des Sciences (Paris)* 303:1393-1396; 1986.
9. Buffetaut, E.; Mechin, P.; & Mechin M.-S.: Un dinosaure théropode d'affinités gondwaniennes dans le Crétacé supérieur de Provence. *Comptes-rendus hebdomadaires des séances de l'Académie des Sciences (Paris)* 306:153-158; 1988.
10. Buffetaut, E.; Meijer, A.W.F.; Taquet, P.; & Wouters, G.: New remains of hadrosaurid dinosaurs (Reptilia, Ornithischia) from the Maastrichtian of Dutch and Belgian Limburg. *Revue de Paléobiologie* 4:65-70; 1985.
11. Bunzel, E.: Die Reptilienfauna der Gosau-Formation in der Neuen Welt bei Wiener-Neustadt. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt Wien* 5:1-18; 1871.
12. Burchfiel, B.C.: Eastern European Alpine system and the Carpathian orocline as an example of collision tectonics. *Tectonophysics* 63:31-61; 1980.
13. Carroll, R.L.: *Vertebrate Paleontology and Evolution*. W.H. Freeman, San Francisco; 1988.

14. Casanovas-Cladellas, M.L.; Santafe-Llopis, J.V.; Sanz, J.L.; & Buscalioni, A.: *Orthomerus* (Hadrosauridae, Ornithopoda) de Cretacico superior de yacimiento de "Els Nerets" (Trempe, Espana). *Paleontologia i Evolució* 19:155-162; 1985.
15. Casanovas-Cladellas, M.L.; Santafe-Llopis, J.V.; Sanz, J.L.; & Buscalioni, A.: *Orthomerus* (Hadrosaurinae, Ornithopoda) du Crétacé supérieur du gisement de "Els Nerets" (Trempe, Lleida). *Les Dinosaurés de la Chine à la France*. Musée d'Histoire Naturelle, Toulouse 99-111; 1985.
16. Casanovas, M.L.; Santafe, J.L.; Sanz, J.L., & Buscalioni, A.D.: Arcosaurios (Crocodilia, Dinosauria) del Cretacico superior de la Conca de Trempe (Lleida, Espana). *Estudios Geologicos*, (volumen extraordinario: Galve-Trempe) 95-110; 1987.
17. Channel, J.E.T.; d'Argenio, B.; & Horvath, F.: Adria, the African promontory. *Earth Science Review* 15:213-292; 1979.
18. Coombs, W.P. Jr.; & Maryánska, T.: Ankylosauria. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
19. Cox, C.B.: Vertebrate distributional patterns and continental drift. *Journal of Biogeography* 1:75-94; 1974.
20. Dercourt, J.; Zonenshain, L.P.; Ricou, L.-E.; et al.: Geological evolution of the Tethys Belt from the Atlantic to the Pamirs since the Lias. *Tectonophysics* 123:241-315; 1986.
21. Gasparini, Z. de; Olivero, E.; Scasso, R.; & Rinaldi, C.: Un ankylosaurio (Reptilia, Ornithischia) Campaniano en el continente Antartico. *Anais X do Congresso Brasileiro de Paleontologia* 131-141; 1987.
22. Gilmore, C.W.: Osteology of the Jurassic reptile *Camptosaurus*, with revision of the species of the genus and description of two new species. *Proceedings of the U.S. National Museum* 36:197-332; 1909.
23. Granger, W.: The story of dinosaur eggs. *Natural History* 38:21-25; 1936.
24. Grigorescu, D.: A stratigraphic, taphonomic and paleoecologic approach to a "forgotten land": the dinosaur-bearing deposits from the Hateg Basin (Transylvania-Romania). *Acta Palaeontologica Polonica* 28:103-121; 1983.
25. Grigorescu, D.: New tetrapod groups in the Maastrichtian of the Hateg Basin: coelurosaurians and multituberculates. Reif, W.-E. & Westphal, R., editors: *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto Verlag, Tübingen; 1984.
26. Grigorescu, D.: Nonmarine Cretaceous formations of Romania. *Symposium on Nonmarine Cretaceous Correlation, International Geological Correlation Program Project 245*; in press.
27. Grigorescu, D.; Seclamen, M.; Norman, D.B.; & Weishampel, D.B.: Dinosaur eggs from Romania. *Nature* 346:417; 1990.
28. Harland, W.B.; Cox, A.V.; Llewellyn, P.G.; et al.: *A Geologic Time Scale*. Cambridge University Press, New York; 1982.
29. Hirsch, K.F.; & Packard, M.J.: Review of fossil eggs and their shell. *Scanning Microscopy* 1:383-400; 1987.
30. Horner, J.R.: Ecological and behavioral implications derived from a dinosaur nesting site. Czerkas, S.J. & Olson, E.C., editors: *Dinosaurs Past and Present*, vol. 2. University of Washington Press, Seattle; 1987.
31. Horner, J.R.; & Weishampel, D.B.: A comparative embryological study of two ornithischian dinosaurs. *Nature* 332:256-257; 1988.
32. Huene, F. von: Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie* (ser. 1) 4:1-361; 1932.
33. Kerourio, P.: Nouvelles observations sur le mode de nidification et de ponte chez les dinosauriens du Crétacé terminal du Midi de la France. *Comptes Rendu Sommaire des Séances, Société Géologique de France* 1981:25-28; 1981.
34. Lapparent, A.F. de.: Les Dinosauriens du Crétacé supérieur du midi de la France. *Mémoires de la Société géologique de France* n.s. 26:1-54; 1947.
35. Lapparent, A.F. de; & Aguire, E.: Algunos yacimientos de Dinosaurios en el Cretacico superior de la Cuenca de Trempe. *Estudios Geologicos* 12:377-382; 1956.
36. Le Loeuff, J.; Buffetaut, E.; Mechin, P.; & Mechin-Salessy, A.: Un arriere-crane de dinosaure titanosauride (Saurischia, Sauropoda) dans le Crétacé supérieur du Var (Provence, France). *Comptes-rendus hebdomadaires des séances de l'Académie Sciences (Paris)* 309:851-857; 1989.
37. Llopart, C.; Casanovas, M.L.; & Santafe, J.V.: Un nuevo yacimiento de Icnitas de Dinosaurios en las facies garum-nienses de la Conca de Trempe (Lleida, Espana). *Acta Geológica Hispánica* 19:143-147; 1984.
38. Llopart, C.; & Kraus, S.: Restos de moluscos y dinosaurios en formaciones estromatolíticas garumniensis al S del Montsec (Prov. de Lérida). *Boletín Geológico y Minero* 93:371-378; 1982.
39. Matheron, P.: Note sur les reptiles fossiles des dépôts fluvio-lacustres crétacés du bassin a lignit de Fuveau. *Bulletin de la Société Géologique de France* (ser. 2) 26:781-795; 1869.
40. McIntosh, J.S.; Sauropoda. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
41. Moisescu, V.: Contributions à la connaissance de la faune de mollusques oligocènes du calcaire dulcaquicole de Merisor (Bassin de Hateg). *Dari de seama, Institutul Geologie-Geofizica, Bucuresti (3-Paleontologie)* 67:99-107; 1982.
42. Molnar, R.E.: An ankylosaur (Ornithischia: Reptilia) from the Lower Cretaceous of southern Queensland. *Memoirs of the Queensland Museum* 20:77-87; 1980.
43. Molnar, R.E.: Problematic Theropoda: "carnosaurs." Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
44. Nopcsa, F.: Vorläufiger Bericht über das Auftreten von oberer Kreide im Hatzeger Tal in Siebenbürgen. *Verhandlungen der Kaiserlich-Königlichen Akademie der Wissenschaften* 273-274; 1897.
45. Nopcsa, F.: Dinosaurierreste aus Siebenbürgen (Schädel von *Limnosaurus transsylvanicus* nov. gen. et spec.). *Denkschriften der Königlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse* 68:555-591; 1900.
46. Nopcsa, F.: Ueber das Vorkommen der Dinosaurier bei Szentpéterfalva. *Zeitschrift der Deutschen Geologischen Gesellschaft* 1902:34-39; 1902.
47. Nopcsa, F.: Dinosaurierreste aus Siebenbürgen II. (Schädelreste von *Mochlodon*). *Denkschriften der königlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse* 72:149-175; 1902.
48. Nopcsa, F.: *Telmatosaurus*, a new name for the dinosaur *Limnosaurus*. *Geology Magazine* (ser. 4) 10:94-95; 1903.
49. Nopcsa, F.: Dinosaurierrest aus Siebenbürgen III. Weitere Schädelreste von *Mochlodon*. *Denkschriften der königlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse* 74:229-263; 1904.
50. Nopcsa, F.: Die Dinosaurier der Siebenbürgischen Landesteile Ungarns. *Mitteilungen aus dem Jahrbuch der Ungarischen Geologischen Reichsanstalt, Budapest* 23:3-24; 1915.
51. Nopcsa, F.: On the geological importance of the primitive reptilian fauna in the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotium*). *Quarterly Journal of the Geological Society of London* 79:100-116; 1923.

52. Nopcsa, F.: Dinosaurierreste aus Siebenbürgen. IV. Die Wirbelsäule von *Rhabdodon* und *Orthomerus*. *Palaeontologia Hungarica* 1:273–304; 1928.
53. Nopcsa, F.: Sexual differences in ornithopodous dinosaurs. *Palaeobiologica* 2:187–200; 1929.
54. Nopcsa, F.: Dinosaurierreste aus Siebenbürgen. V. *Geologica Hungarica* 4:1–76; 1929.
55. Nopcsa, F.: The influence of geological and climatological factors on the distribution of non-marine fossil reptiles and Stegocephalia. *Quarterly Journal of the Geological Society of London* 90:76–140; 1934.
56. Norman, D.B.: On the ornithischian dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Institut Royal des Sciences Naturelles de Belgique. Mémoires* 178:1–105; 1980.
57. Norman, D.B.: On the cranial morphology and evolution of ornithopod dinosaurs. *Symposium of the Zoological Society of London* 52:521–547; 1984.
58. Norman, D.B.: On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal d'Histoire Naturelle de Belgique* 56:281–372; 1986.
59. Norman, D.B.; & Weishampel, D.B.: Iguanodontidae and related ornithopods. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
60. Osmólska, H.; & Barsbold, R.: Troodontidae. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
61. Paris, J.-P.; & Taquet, P.: Découverte d'un fragment de dentaire d'Hadrosaurien (Reptile, Dinosaurien) dans le Crétacé supérieur des Petites Pyrénées (Haute-Garonne). *Bulletin du Musée National d'Histoire Naturelle* 22:17–27; 1973.
62. Pop, G.; Negagu, T.; & Szasz, L.: Senonianul din regiunea Hategului (Carpatii Meridionale). *Dari de seama, Institutul Geologie-Geofisica, Bucuresti (4-Stratigrafie)* 5:95–118; 1972.
63. Riabinin, A.N.: Ostatki dinosavra iz verkhnego mela Krima. *Material Vsesoyuznogo nauchnoissled geologorazvedotschnogo inta, Paleontologiya i Stratigrafiia, Sbornik* 4:4–10; 1945.
64. Romer, A.S.: *Osteology of the Reptiles*. University of Chicago Press, Chicago; 1956.
65. Romer, A.S.: *Vertebrate Paleontology*. University of Chicago Press, Chicago; 1966.
66. Sanz, J.L.; & Buscalioni, A.D.: New evidence of armoured dinosaurs in the Upper Cretaceous of Spain. Currie, P.M. & Koster, E.H., editors: *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Tyrrell Museum of Palaeontology, Drumheller, Alberta; 1987.
67. Seeley, H.G.: The reptile fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. With a note on the geological horizon of the fossils at Neue Welt, west of Wiener Neustadt, by Edw. Suess. *Quarterly Journal of the Geological Society of London* 37:620–707; 1881.
68. Sereno, P.C.: Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research* 2:234–256; 1986.
69. Sues, H.-D.; & Norman, D.B.: Hypsilophodontidae, *Tenontosaurus*, *Dryosauridae*. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
70. Taquet, P.: Géologie et paléontologie du gisement de Gadoufaoua (Aptian du Niger). *Cahiers de Paléontologie*. Centre National de la Recherche Scientifique, Paris; 1976.
71. Tollman, A.: Die alpidischen Geburbsbildungsphasen in den Ostalpen und Westkarpaten. *Geotektonische Forschung* 21:1–156; 1966.
72. Villatte, J.; Taquet, P.; & Bilotte, M.: Nouveaux restes de dinosauriens dans le Crétacé terminal de l'anticlinal de Dreuilhe. État des connaissances dans le domaine sous-pyrénéen. *Les Dinosauriens de la Chine à la France*. Toulouse, 89–98; 1985.
73. Weishampel, D.B.: Evolution of jaw mechanisms in ornithopod dinosaurs. *Advances in Anatomy, Embryology, and Cell Biology* 87:1–110; 1984.
74. Weishampel, D.B.: Dinosaurian distribution. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
75. Weishampel, D.B.; & Bjork, P.R.: The first indisputable remains of *Iguanodon* (Ornithischia: Ornithopoda) from North America: *Iguanodon lakotaensis*, sp. nov. *Journal of Vertebrate Paleontology* 9:56–66; 1990.
76. Weishampel, D.B.; & Horner, J.R.: The hadrosaurid dinosaurs from the Iren Dabasu fauna (People's Republic of China, Late Cretaceous). *Journal of Vertebrate Paleontology* 6:38–45; 1986.
77. Weishampel, D.B.; & Horner, J.R.: Hadrosauridae. Weishampel, D.B., Dodson, P., & Osmólska, H., editors: *The Dinosauria*. University of California Press, Berkeley; 1990.
78. Weishampel, D.B.; & Reif, W.E.: The work of Franz Baron Nopcsa (1877–1933): dinosaurs, evolution and theoretical tectonics. *Jahrbuch der Geologischen Bundesanstalt* 127–203; 1984.
79. Weishampel, D.B.; & Weishampel, J.B.: Annotated localities of ornithopod dinosaurs: implications to Mesozoic paleobiogeography. *Mosasaurs* 1:43–87; 1983.
80. Westphal, M.; Bazhenov, M.L.; Lauer, J.P.; et al.: Paleomagnetic implications on the evolution of the Tethys belt from the Atlantic Ocean to the Pamirs since the Triassic. *Tectophysics* 123:37–82; 1986.
81. Young, C.C.: Fossil eggs from Nan-hsiung, Kwangtung and Kanchou, Kiangsi. *Vertebrata Palasiatica* 9:141–170; 1965.

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