

TELMATOSAURUS TRANSYLVANICUS FROM THE LATE CRETACEOUS OF ROMANIA: THE MOST BASAL HADROSAURID DINOSAUR

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ABSTRACT. The hadrosaurid dinosaur *Telmatosaurus transylvanicus* from the Late Cretaceous of the Hațeg region of Romania is redescribed and its phylogenetic position among hadrosaurids and successive sister-taxa is evaluated. Hadrosauridae is defined and diagnosed as a monophyletic group on the basis of twelve of the best-known genera and species previously referred to this higher taxon. *T. transylvanicus* lacks a number of features (among them, narrow mandibular condyle of the quadrate, narrow dentary teeth, single large carina on dentary teeth) that diagnose remaining members of Hadrosauridae. As a consequence, our study indicates that *T. transylvanicus* is the most basal of known hadrosaurids. The late Maastrichtian age of *T. transylvanicus* suggests that this species was an evolutionary relict, isolated from its sister taxon (all remaining hadrosaurids) for at least fifteen million years. The geographical distribution of *T. transylvanicus*, across an archipelago of European islands at the end of the Cretaceous, may well account for such an evolutionary relationship.

WHEN Ilona Nopcsa, the sister of Franz Baron Nopcsa, discovered remains of hadrosaurid dinosaurs on their Transylvanian estate in 1895, only twenty-four species of these ornithomimid dinosaurs were known elsewhere in the world. Since 1899, when Franz Baron Nopcsa reported on these specimens before the Viennese Academy of Sciences (Nopcsa 1900), the majority of early-named hadrosaurid species have been ignominiously relegated to the taxonomic scrap-heap (Weishampel and Horner 1990). Nopcsa's species from Transylvania, however, is one of the survivors of modern revisions.

This hadrosaurid from the Hațeg Basin of western Romania was originally named *Limnosaurus transylvanicus* (Nopcsa, 1900). Because the name *Limnosaurus* was preoccupied by a fossil crocodylian (Marsh 1872), Nopcsa (1903) replaced it with *Telmatosaurus* (see Paris and Taquet 1973; Weishampel and Reif 1984; Brinkmann 1988). The holotype and referred material of *T. transylvanicus* range from nearly complete, isolated cranial specimens to isolated axial and appendicular elements. On the basis of the preservation, completeness, and abundance of this material, *Telmatosaurus transylvanicus* ranks as one of the best-known dinosaur taxa from Romania, and perhaps even all of Europe, during the Late Cretaceous.

Despite these claims, *T. transylvanicus* was not included in several important reviews of hadrosaurid taxonomy and systematics (e.g. Lull and Wright 1942; Ostrom 1961; but see Brinkmann 1988). These studies were restricted solely to consideration of North American taxa, for which there is considerably better preserved and more diverse material. As a consequence, *T. transylvanicus* has also not been featured in studies of Late Cretaceous faunistics, palaeoecology, and biogeography, nor in the controversies about Cretaceous–Tertiary extinction patterns.

Earlier we presented some of the historical context of work on the Hațeg fauna (Weishampel *et al.* 1991; see also Weishampel and Reif 1984). Most early work centred on Nopcsa's detailed taxonomic work on the dinosaurs from the Sînpetru Beds (now split into the Sînpetru and Densuș-Ciula formations), but also included his synthetic work on the island biogeography of these same animals. At the end of Nopcsa's life, the fauna included a number of dinosaurs (*Telmatosaurus transylvanicus*, *Rhabdodon priscus*, 'Struthiosaurus' *transilvanicus*, *Magyarosaurus dacus*, *Meg-*

alosaurus hungaricus), a crocodile (*Allodaposuchus precedens*), a turtle (*Kallokibotion bajazidi*), and a pterosaur, the material of which is presently missing.

Very little sustained field research was conducted in the Hațeg Basin from the time of Nopcsa's death in 1933 until work by the Universitatea București in the mid-1970s. This most recent work in Transylvania, under the direction of one of us (D.G.), has considerably enlarged the fauna. In addition to what had been known previously, new taxa included acipenseriform and characid fishes, amphibians, a species of multituberculate mammal (*Paracimexomys? dacicus*), large and small theropod dinosaurs, hatchling ornithopod dinosaurs, and dinosaur eggs (Grigorescu *et al.* 1990, in press; Weishampel *et al.* 1991).

Our review of the osteology of *Telmatosaurus transsylvanicus* is based on material originally collected by Ilona and Franz Baron Nopcsa in the late nineteenth and early twentieth century, by Kadić O. in 1914, and by the Universitatea București since the 1970s. The goal of this study is to place *T. transsylvanicus* in its proper phylogenetic position and thereby address its importance to Late Cretaceous palaeoecology and biogeography.

ABBREVIATIONS

BMNH, Natural History Museum, London, England; FGGUB, Facultatea de Geologie și Geofizică, Universitatea București, Bucharest, Romania; MAFI, Magyar Állami Földtani Intézet, Budapest, Hungary; MJH, Muzeul Județean Hunedoara, Deva, Romania; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNMB, Magyar Nenzeti Múzeum, Budapest, Hungary; PIN, Palaeontologiceski Institut, Akademii Nauk, Moscow, Russia; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

SYSTEMATIC PALAEOLOGY

ORNITHOPODA Marsh, 1881

Family HADROSAURIDAE Cope, 1869

Genus TELMATOSAURUS Nopcsa, 1903

Telmatosaurus transsylvanicus (Nopcsa, 1900)

Text-figs 1–6

Holotype. BMNH R3386, a relatively complete, but crushed skull.

Referred material. BMNH R2967, R3387, R3388, R3401, R3809, R3828, R3841, R3842, R3843, R3844, R3845, R3846, R3847, R3848, R4878, R4879, R4897, R4910, R4911, R4913, R4914, R4915, R4973, R5614, R10981, R10983, R11108, R11109, R11110, R11111, R11112, R11113, R11114, R11539, R11545, FGGUB 1000, 1005, 1006, 1008, 1010, 1015, 1018, 1033, 1040, 1051, 1078, [4], [5], [11], [15], [24], [40], [42], MAFI Ob.1943, Ob.3079, Ob.3107, Ob.3108, Ob.3109, Ob.3110, Ob.3111, Ob.3112, Ob.3113, Ob.3115, Ob.3116, Ob.3117, Ob.3118, Ob.3120, Ob.3121, Ob.3122, Ob.3123, Ob.3124, Ob.3126, Ob.3127, Ob.3128, Ob.3129, Ob.3130, Ob.3283, Ob.3284, Ob.4212, v.10338, v.13495, v.13497, v.13503, v.13504, v.13526, v.13513, MJH 66, 70, MNMB v.60. These specimens consist of isolated cranial elements, articulated and isolated cervical, dorsal, sacral, and caudal vertebrae, and various appendicular elements including scapulocoracoid, humerus, ulna, femur, tibia, and pedal elements. Referral of these postcranial elements to *T. transsylvanicus* is based principally on Nopcsa's personal account of their association (through notes, museum acquisition records, and publications).

Provenance. Sînpetru and Densuș-Ciula formations, Upper Maastrichtian; Hațeg Basin, Județul Hunedoara, Romania.

Diagnosis. A hadrosaurid dinosaur (see Weishampel and Horner 1990 for familial diagnosis) of small body size (a dwarf?), having a large caudal ectopterygoidal shelf, an isosceles triangle-shaped rostral process of the jugal, a relatively long post-metotic braincase, relatively large basiptyergoid processes, a relatively large scar for *m. protractor pterygoideus* on the lateral aspect of the

basisphenoid, a well-developed channel for the palatine branch of the facial nerve that also accommodated the median cerebral vein, absence of a diastema between the predentary and dentary dentition, and a slightly bowed femur.

DESCRIPTION

Skull, mandible, and dentition

Although the most complete cranial material of *T. transsylvanicus* is the crushed holotype (BMNH R3386), referred material was used in conjunction with this deformed specimen to reconstruct the undistorted skull of this species (Text-fig. 1; see also Weishampel *et al.* 1991). The following description is based on both sources. Except where noted, all measurements are taken from the reconstructed skull.

In lateral view (Text-fig. 1A), the undistorted skull of *T. transsylvanicus* is relatively long (440 mm) compared with its height (215 mm, measured from the mandibular condyle of the quadrate to the top of the skull roof). Such skull proportions are similar to those of *Camptosaurus dispar*, species of *Iguanodon*, and *Ouranosaurus nigeriensis*, while different from many hadrosaurids. The dorsal margin of the skull rises in a gentle curve from the muzzle to immediately over the orbits. In dorsal view (Text-fig. 1B; see also Weishampel *et al.* 1991), the muzzle itself is approximately 85 mm at its widest, while across the orbits and adductor chambers it is 185 mm wide. In caudal view, the skull is at least 175 mm wide (measured across preserved portions of the squamosals).

Although known from the majority of cranial elements, existing material of *T. transsylvanicus* does not include the prefrontal (nor a palpebral, should one have existed), most of the postorbital, the quadratojugal, portions of the jugal, most of the palate, and the predentary. Most of the braincase is preserved, but intracranial sutures tend to be fused and/or obliterated by maturity and/or erosion of the specimens. However, using comparative material, it is possible to reconstruct the braincase of *T. transsylvanicus* (Text-fig. 2) with some confidence.

We begin our description of the skull of *T. transsylvanicus* with elements of the facial skeleton, continuing with the braincase, palate, and mandible.

Premaxilla. In dorsal view, the premaxilla of *T. transsylvanicus* (BMNH R3386, R3842, R4911; FGGUB 1008, 1015) is not particularly expanded (Text-fig. 1B). In this feature, it is more like *Camptosaurus dispar* and species of *Iguanodon* (Gilmore 1909; Norman 1980, 1986; Weishampel and Bjork 1989) than *Ouranosaurus nigeriensis* and other hadrosaurids. In lateral view, the ventral margin of the premaxilla is depressed well beneath the level of the maxillary tooth row.

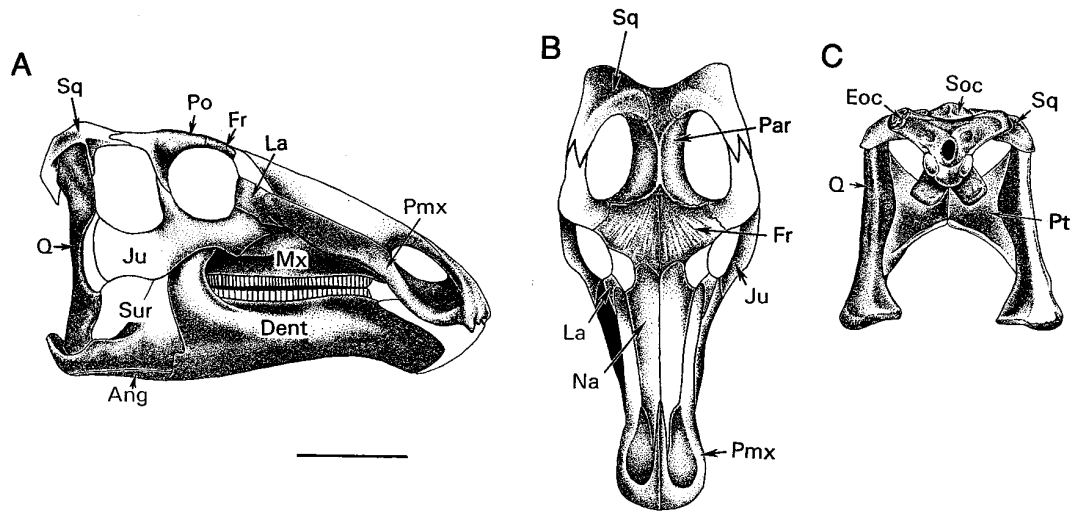
The oral margin of the premaxilla is strongly denticulate (Text-fig. 3A-B), again reminiscent of that found in *Iguanodon atherfieldensis*, *I. bernissartensis*, *I. lakotaensis*, and *Ouranosaurus nigeriensis* (Taquet 1976; Norman 1980, 1986; Weishampel and Bjork 1989). These denticles are restricted to the more medial aspect of the oral margin of the premaxilla; in BMNH R3386, there are three projections on each premaxilla, while in FGGUB 1015 there are two. In addition, the oral margin and adjacent rostral surface of the premaxilla is roughened by short, vertical striations and pitting, suggesting a rhamphothecal covering in life.

The body of the premaxilla flares slightly to form an approximately horizontal floor for the narial fossa (Text-fig. 3A). Within the fossa, the external nares are relatively small and forwardly placed on the muzzle. There is no evidence of a circumnarial depression. Extending caudally from the floor of the narial fossa, the caudolateral process of the premaxilla extends to and subsequently laps the lateral surface of the lacrimal. Thus, the nasal and maxilla are separated by the premaxilla in lateral view (BMNH R3386).

The ventral surface of the premaxilla is perforated by a premaxillary foramen (*sensu* Horner 1983). This foramen (not seen in BMNH R3386, but visible in FGGUB 1008 and 1015; Text-fig. 3B) enters the central portion of the premaxilla, about 12 mm from the interpremaxillary suture (FGGUB 1008). It is not clear from currently known material whether this foramen communicates via a canal with the narial fossa.

Nasal. Although dorsoventrally crushed, the nasal does not appear to be strongly arched in BMNH R3386 (nor in a specimen from the Upper Cretaceous of southern France here referred to *Telmatosaurus*, MNHN FMR 12). Instead, it continues the gentle upward slope of the muzzle that was established by the dorsal margin of the premaxilla (Text-fig. 1A).

Frontal. In dorsal view, the frontal of *T. transsylvanicus* (BMNH R3386, R3828, R4911, R4915) is a relatively flat, triangular element (Text-fig. 1B). The paired frontals are unfused, but form a slightly sinuous interfrontal suture. Along the forward edge, there are deep excavations to receive the caudal ends of the nasal and



TEXT-FIG. 1. *Telmatosaurus transsylvanicus*. A–C, skull in right lateral, dorsal, and caudal views respectively. All figures based in large part on BMNH R3386 and R3387. Scale = 100 mm. A–B after Weishampel *et al.* 1991. Abbreviations: Ang = angular; Dent = dentary; Eoc = exoccipital; Fr = frontal; Ju = jugal; La = lacrimal; Mx = maxilla; Par = parietal; Pmx = premaxilla; Po = postorbital; Pt = pterygoid, Q = quadrate; Soc = supraoccipital; Sq = squamosal; Sur = surangular.

prefrontal. The margin of the excavation for the nasal is slightly raised in BMNH R4915. Medially, the paired frontals extend between the nasals as an oblique wedge. Ventrally, divergent ridges mark the suture between the frontal and laterosphenoid and the margins of the olfactory tracts.

The lateral edge of the frontal forms of the forward half of the orbital rim (Text-fig. 1A), as in *Gryposaurus notabilis*, *G. incurvimanus*, *Anatotitan copei*, and species of *Edmontosaurus*, among hadrosaurids, and virtually all other iguanodontians (e.g. *Camptosaurus dispar*, species of *Iguanodon*). Caudally and laterally, the frontal–postorbital suture is interdigitate and extends rostromedially from the forward margin of the supratemporal fenestra. The frontal–parietal articulation sweeps across the skull roof (also in an interdigitate fashion) to meet the frontal–postorbital suture along the rim of the supratemporal fenestra. There is no evidence of a medial gap accommodating an extension of the parietal (the ‘interparietal’ process *sensu* Lull and Wright 1942). Immediately rostral to the frontal–parietal articulation, the frontal is raised into a low transverse ridge.

Parietal. The parietals are fused into a single plate (known only in BMNH R3386) which is relatively long (90 mm), suggesting that the adductor chamber was large (Text-fig. 1B), as in *Camptosaurus dispar* and species of *Iguanodon*, and *Gryposaurus notabilis*, *G. incurvimanus*, and *Kritosaurus navajovius* among other hadrosaurids (Horner 1992). In *T. transsylvanicus*, there is a modest sagittal crest. In dorsal view, the parietal is hour-glass shaped. Rostrally, it is bounded by the frontal and postorbital, while caudally it articulates with the squamosal and supraoccipital. Ventrally, the parietal articulates with the laterosphenoid, prootic, and opisthotic.

Postorbital. Only the most rostral portion of the postorbital, where it contacts the frontal (see above), is known in *T. transsylvanicus*. Morphological details beyond those already given are non-existent.

Squamosal. The squamosal is incompletely known (BMNH R3386; Text-fig. 1A). Missing are the rostral process (which contacts the postorbital) and most of the medial process (which contacts the parietal and paroccipital process). The body of the squamosal forms a deep cotylus for reception of the head of the quadrate. The base of the prequadrate process preserves the scar for *m. adductor mandibulae externus superficialis*.

Maxilla. The maxilla (Text-fig. 3c) is known from a number of specimens, among them FGGUB 1010, MAFI Ob.3108, Ob.3109, and BMNH R3386, R3388, R4911, R5164. This triangular element is relatively long and low (195 mm and 70 mm respectively for FGGUB 1010). The dorsal process is located approximately halfway along the length of the maxilla. Rostral to the dorsal process, the concave dorsal surface of the maxilla receives the caudal portion of the body and caudolateral process of the premaxilla. Because of poor preservation, it is unclear whether a rostromedial maxillary process was present in *T. transsylvanicus*. Immediately lateral to the dorsal maxillary process is the articular surface for the jugal. This nearly triangular surface is slightly offset from the lateral surface of the maxilla. However, unlike other hadrosaurids, there is not much scarring in this region.

The lateral wall of the maxilla bears no indication of a laterally-positioned antorbital fenestra and fossa. Instead, the more caudal region of the premaxillary articular surface contains a relatively large, oval foramen that communicates with the region behind the dorsal maxillary process. This foramen has been argued to be the antorbital foramen among hadrosaurids (Weishampel and Horner 1990). A series of foramina mark the lateral surface of the maxilla, the largest of which is beneath and slightly forward of the articular surface for the jugal. Together, these foramina fall irregularly in a longitudinal row and probably represent neurovascular canals that conduct branches of the maxillary nerve and vessels to the buccal cavity and cheek region, as in other ornithischians. Beneath this position, the maxilla becomes slightly emarginated, such that the maxillary dentition is inset from the side of the face.

Caudal to the dorsal process and jugal articular surface, the maxilla bears a prominent ectopterygoid shelf. This shelf is relatively broad and slightly undulatory, thus producing a slightly bulbous caudal extreme. Medial to the ectopterygoid shelf, the maxilla is drawn up into a well-striated edge that supports the base of the palatine (BMNH R3388, R4911). The medial side of the maxilla is relatively flat and covered by an arc of special foramina (Edmund 1957) that mark the base of each alveolar chamber.

Ventrally, the maxillary tooth row is laterally concave, much as in *Iguanodon atherfieldensis* and hadrosaurids generally. It contains more tooth positions than more basal iguanodontians of approximately the same size (cf. 31 in FGGUB 1010, 19 in *Iguanodon lakotaensis*, 22 in *Ouranosaurus nigeriensis*) and about the same as other similar-sized hadrosaurids (approximately 30 in *Gilmoresaurus mongoliensis*, 35 in *Prosaurolophus maximus*).

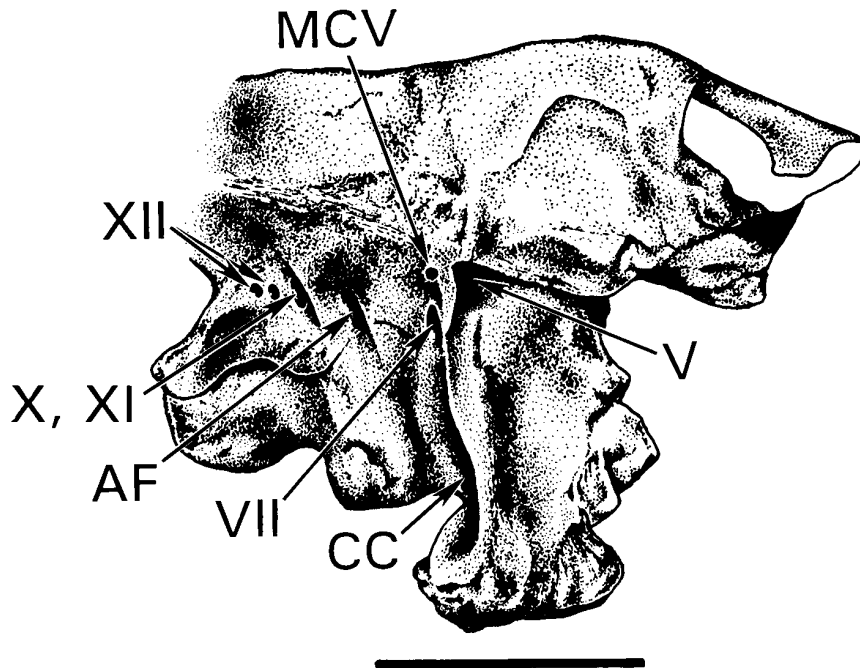
Lacrimal. Much of the detail of the lacrimal is lost as the result of crushing in BMNH R3386, the only specimen preserving this element. Nonetheless, it appears to be typically triangular, overlapped rostrally by the caudolateral process of the premaxilla (Text-fig. 1A).

Jugal. The rostral portion of the jugal (BMNH R3386, R4911, R11545; Text-fig. 1A) appears to form an isosceles-triangle-like articulation with the maxilla. The inner surface of this rostral portion is strongly striated for ligaments that tightly bound the jugal to the maxilla. The postorbital process is best preserved (albeit poorly) in BMNH R4911. Beneath this process, the body of the jugal is dorsoventrally narrow, giving a very gracile form to the bone when compared to other hadrosaurids. The caudal portion of the jugal is unknown.

Quadrate. The quadrate of *T. transsylvanicus* is known from a number of specimens (FGGUB 1005, 1006; BMNH R3386, R4911; Text-fig. 3D). The head of the quadrate is relatively narrow transversely and shallowly curved in lateral view. The caudal aspect of the quadrate head bears a buttress that lies against the rostrolateral surface of the paroccipital process. More ventrally, the shaft is relatively straight. Above the mandibular condyle, the cranial margin of the shaft is excavated for reception of the quadratojugal. However, there appears to be no paraquadratic foramen. Directly beneath this excavation, there is again a slight buttress similar to that found in the hadrosaurid *Gilmoresaurus mongoliensis*. The transversely broad mandibular condyle resembles the condition in *Camptosaurus dispar*, species of *Iguanodon*, *Ouranosaurus nigeriensis*, and *Gilmoresaurus mongoliensis*, but differs from the more rounded and narrow condition found in all remaining hadrosaurids.

Supraoccipital. The supraoccipital (Text-fig. 1c) is lodged between the squamosals, the parietal, and the exoccipitals within the dorsal region of the occiput (BMNH R3386, R3387, R3401). Lateral facets on the supraoccipital articulate with the medial process of the squamosal. Immediately ventral to each facet is the relatively large post-temporal foramen which transmitted the dorsal head vein between the supraoccipital, opisthotic, and squamosal.

Exoccipital. In caudal view (Text-fig. 1c), the exoccipital forms the dorsal margin of the foramen magnum as well as the majority of the occipital table (i.e. BMNH R3386, R3387, R3401). Ventrally, the well-developed



TEXT-FIG. 2. *Telmatosaurus transylvanicus*. Braincase in right lateral view. Reconstructed after BMNH R3386, R3401, R3387, R4915. Scale = 50 mm. Abbreviations: AF = auditory foramen; CC = carotid canal; MCV = foramen for the median cerebral vein; V, VII, X, XI, XII: foramina for cranial nerves.

exoccipital condyloids supplement the basioccipital condyle where it forms the craniovertebral joint with the atlas.

In the centre of the caudal surface of the exoccipital is a scar for *m. obliquus capitis magnus*. The base of the paroccipital process is found immediately lateral to this scar, but the extreme lateral aspect of the exoccipital is not preserved in any existing material. Hence, it is unclear how well developed the paroccipital processes were in life. Furthermore, the sutures with the opisthotic are entirely obliterated in both caudal and lateral views, so it is unclear as to the extent that either the exoccipital or opisthotic form the paroccipital process.

The lateral wall of the exoccipital is exposed in lateral view (Text-fig. 2). Here the base of the exoccipital makes an undulatory contact with the basioccipital. The exoccipital appears to meet the basisphenoid immediately caudal and ventral to the auditory foramen. Based on BMNH R4915, the lateral wall of the exoccipital contains the foramina for several cranial nerves. The exit for the hypoglossal nerve (c.n. XII) is unclear, but may be found approximately two-thirds along the length of the exoccipital. Whether there is a single exit or two is not known (two are reconstructed in Text-figure 2). Immediately rostral, the foramen that transmitted the spinal accessory and vagus nerves (c.nn. X, XI) is separated by a prominent pillar from the auditory foramen. This pattern of cranial foramina through the body of the exoccipital is also seen in other hadrosaurids (Horner 1992), but differs from that of *Iguanodon atherfieldensis*, *I. lakotaensis* (Norman 1986; Norman and Weishampel 1990), and possibly *Ouranosaurus nigeriensis* (Taquet 1976), where these same foramina are found along the suture between the exoccipital and opisthotic.

Opisthotic. As indicated above, the boundaries of the opisthotic are not easily demonstrated, but presumably the element comprises the caudal portion of the otic (i.e. caudal to the metotic fissure) and the extreme portion of the paroccipital process.

The lateral wall of the opisthotic is marked by the caudal half of the crista otosphenoidale as it extends into the rostromedial surface of the paroccipital process (Text-fig. 2). At the base of the crista otosphenoidale, where it continues onto the prootic, the opisthotic is pierced by the auditory foramen at the level of the metotic

fissure. Dorsally, this foramen accommodates the foot plate of the stapes, while ventrally, the glossopharyngeal nerve (c.n. IX) and the jugular vein exit the braincase. A shallow groove for the jugular vein extends ventrally from the auditory foramen across the lateral surface of the basisphenoid. Both groove and foramen are shrouded rostrally by a pillar that separates both from the foramen accommodating the facial nerve (c.n. VII).

Prootic. As indicated above, the crista otosphenoidale terminates rostrally in the caudoventral corner of the prootic (Text-fig. 2). The foramen for the facial nerve (c.n. VII) is probably positioned above the foramen for c.n. VI and caudal to the foramen for c.n. V. It is likely that the middle cerebral vein pierces the lower body of the prootic or the junction between the prootic and laterosphenoid immediately dorsal to the exit of c.n. VII. Finally, the rostroventral margin of the prootic forms the dorsal and caudal margins of the exit for the trigeminal nerve (c.n. V).

Laterosphenoid. The pillar-like laterosphenoid extends rostrolaterally from the front of the braincase (Text-fig. 2) to abut the undersurface of the postorbital and frontal in what appears to be a synovial joint (Weishampel 1984). The olfactory tract (c.n. I) exits between the paired laterosphenoids.

Orbitosphenoid. The orbitosphenoid (Text-fig. 2) is extremely poorly preserved and provides no information on the foramina for the trochlear nerve (c.n. IV) or the palatine artery, two structures expected to be found in this region of the braincase.

Basioccipital. The basisphenoid contributes the largest portion of the occipital condyle and forms as much as a sixth of the (ventral) rim of the foramen magnum (Text-fig. 1c). The occipital condyle is supported rostrally by a modest neck. The most rostral portion of the basioccipital forms the caudal third of the rugose basal tuber (the remainder is formed by the basisphenoid; see below). At the ventral limit of the suture between the basioccipital and basisphenoid is a small, shallow fossa that appears to be shared by both the basioccipital and basisphenoid. This fossa may mark the attachment site of *m. rectus capitis rostralis*.

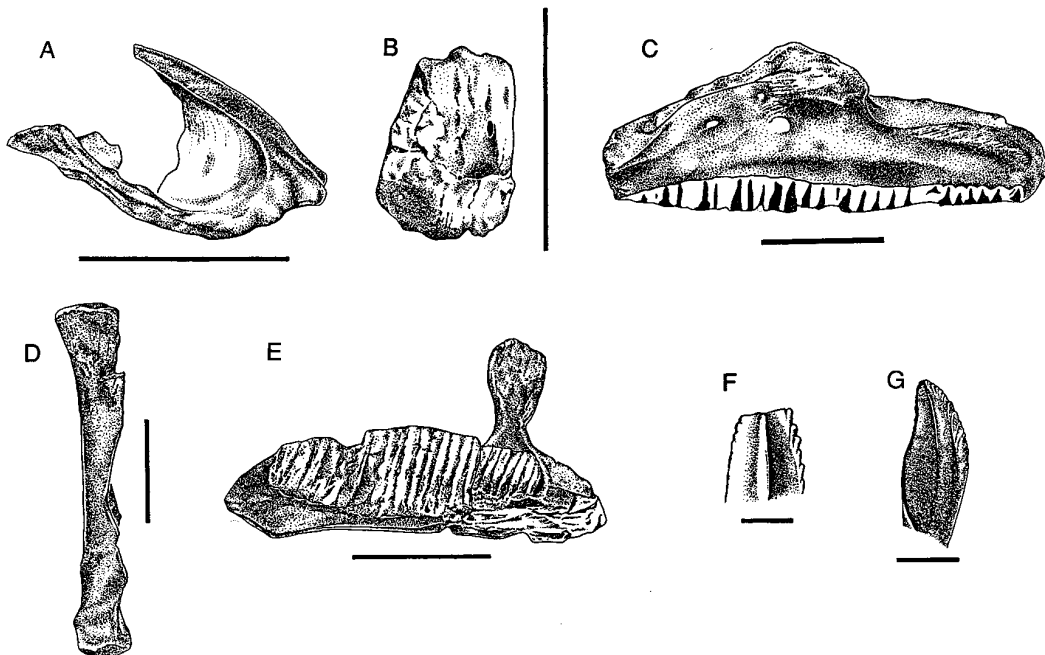
Basisphenoid. The basisphenoid (Text-fig. 2) forms the rostral two-thirds of the large basal tuber, which projects ventrally approximately 40° from the midline. Likewise, the basipterygoid processes are relatively large, although incompletely preserved. At the base of each process is the opening of the carotid canal. This opening also marks the terminus of a channel descending from the facial nerve foramen. This wide and slightly sinuous channel presumably contained the palatine branch for the facial nerve and probably also the median cerebral vein prior to its union with the lateral head vein.

As noted earlier, the foramina for the median cerebral vein and trigeminal nerve are poorly preserved in existing *T. transsylvanicus* material. However, a large gap between the laterosphenoid, prootic, and basisphenoid (see BMNH R3386, R4915) assuredly accommodated both structures as indicated in Text-figure 2. Extending ventrally from the trigeminal foramen, immediately rostral to the channel for the palatine branch of the facial nerve, is a moderately-developed groove for the maxillary and mandibular branches of the trigeminal nerve (c.n. V_{2,3}). Another groove extending rostrally from the trigeminal foramen accommodated the ophthalmic branch of the trigeminal nerve. Both sets of grooves for branches of the trigeminal nerve flank the relatively large scar for *m. protractor pterygoideus*.

Pterygoid. Of the palate, only the pterygoids are at all easily identifiable (although extremely crushed) in BMNH R3386. The strongly developed caudoventral projection of the quadrate ramus extends laterally to contact the medial aspect of the quadrate shaft, while the caudal alar projection is typically thin and high (Text-fig. 1c). The remainder of the pterygoid, including the articulation with the basipterygoid process of the basisphenoid, are very fragmentary due to crushing.

Dentary. The dentary is known from a number of specimens (MAFI Ob. 1943; BMNH R2967, R3386, R3401, R3844, R4910; Text-figs 1, 3E). In the region where it contacts the prementary, the rostral end of the dentary bends ventrally and medially to form the mandibular symphysis. There appears to be no more than a small diastema between the prementary (estimated from the prementary articular surface on the dentary) and the first dentary tooth.

In lateral view, the body of the dentary is roughly rectangular, with parallel dorsal and ventral margins. The dentition is emarginated from the lateral surface. In the largest dentary (BMNH R3386), there are approximately 30 tooth positions. Replacement teeth are arranged in a dental battery, typical of hadrosaurid dinosaurs. A series of foramina is irregularly placed in nearly a longitudinal row beneath the tooth row. These



TEXT-FIG. 3. *Telmatosaurus transsylvanicus*. A-B, right premaxilla (FGGUB 1015) in lateral and ventral views. C, left maxilla (FGGUB 1010) in lateral view. D, right quadrate (FGGUB 1005) in lateral view. E, right dentary (BMNH R3401) in medial view. F, tooth (BMNH R4966) from the left maxilla in buccal view. G, tooth (FGGUB [5]) from the right dentary in lingual view. Scales for A-E = 50 mm; scale for F = 5 mm; scale for G = 10 mm. (G after Weishampel *et al.* 1991).

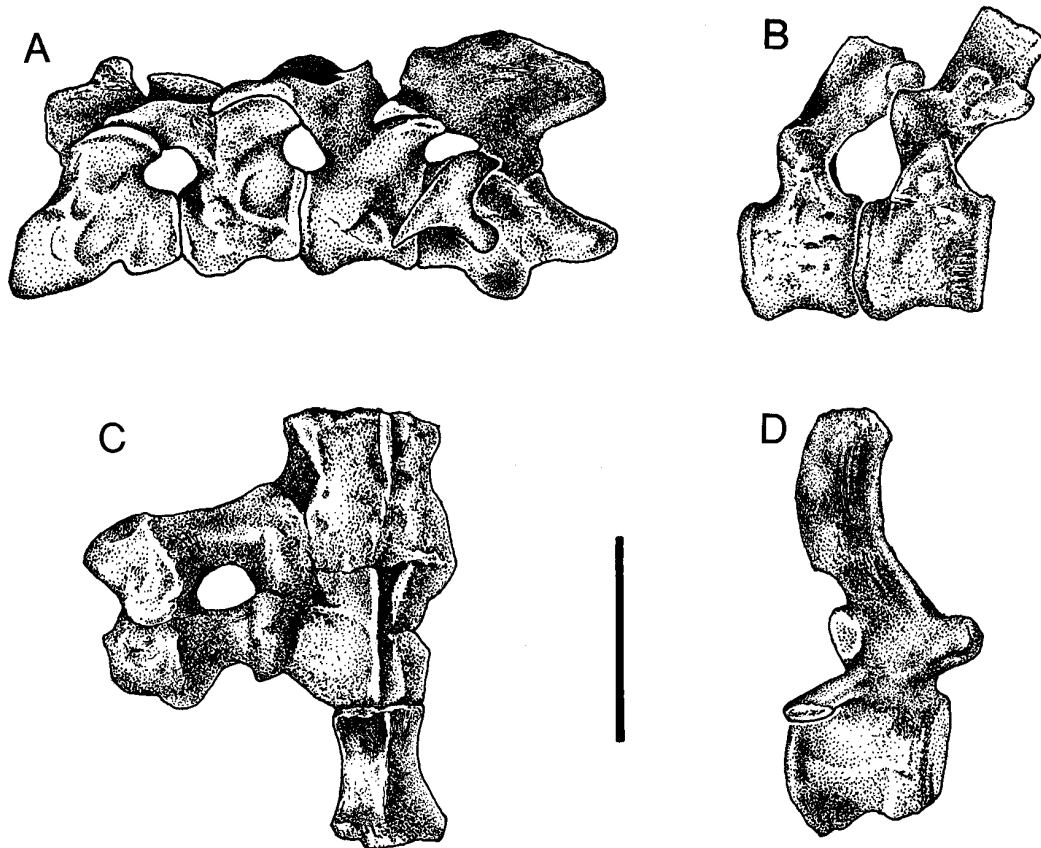
foramina attest to neurovascular supply to the lower regions of the buccal cavity and cheek via the mandibular branch of the trigeminal nerve (c.n. V_3). The largest of these foramina is found near the articular surface for the lateral process of the prementary. Such a position indicates a particularly important neurovascular supply to the prementary portion of the oral margin.

Immediately lateral to the distal limit of the dentary dentition, the coronoid process rises 35 per cent higher than the height of the body of the dentary. The coronoid process forms a 105° angle with the long axis of the dentary. Dorsally, the coronoid process flares into a marked coronal margin. Caudally, the base of the coronoid process is excavated to form the mandibular fossa, which continues rostrally as the mandibular canal (seen in medial view). The surangular comprises the caudal continuation of the lateral wall of the mandibular fossa.

The medial wall of the dentary bears a series of special foramina (*sensu* Edmund 1957) at the base of the alveolar chambers. Immediately caudal to the dental battery and these special foramina, the dentary forms a squamous, rostrally crescentic suture with the splenial. Beneath this position, the dentary contacts the angular ventral to the mandibular canal.

Surangular. The large surangular (Text-fig. 1A; see BMNH R3386, R4911; MAFA Ob.3123, v.13497) forms the caudal part of the coronoid process, the large, lateral aspect of 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. There is no surangular foramen. Beneath the glenoid, the ventral surface of the surangular is undulatory. More caudal, the retroarticular process of the surangular is upturned and lobate. The caudoventral margin of the angular fits into a groove on the ventral surface of the surangular.

Splenial. The splenial forms the medial wall of the mandibular fossa beginning at the caudal limit of the dentary



TEXT-FIG. 4. *Telmatosaurus transsylvanicus*. A, axis and next three cervical vertebrae (BMNH R3841) in right lateral view. B, last cervical and first dorsal vertebrae (BMNH 3841) in left lateral view. C, sacrum (BMNH R4911) in ventral view; D, isolated proximal caudal vertebra (BMNH R4973) in right lateral view. Scale = 50 mm.

dentition. Further posteriorly, the junction between the splenial and the articular is indistinct, suggesting that both elements may fuse.

Angular. The angular is a long, narrow mandibular element that forms the floor of the mandibular fossa and the mandibular canal. Medially, it forms a long, linear suture with the splenial, while laterally, it develops a similar articulation with the dentary and surangular.

Articular. The articular forms a broad squamous joint with the surangular, thereby contributing the smaller, more medial aspect of the mandibular glenoid. The portion of the glenoid is also enclosed medially by a rounded lip. The articular also contributes the inner surface of the retroarticular process.

Dentition. Both maxillary and dentary dentitions are organized into dental batteries. Maxillary batteries consist of one to two functional teeth and up to three replacement teeth per tooth position, while two to three functional teeth and an estimated four to five replacement teeth per tooth position occupy the dentary. Maxillary teeth are high and relatively narrow in cross-sectional dimensions (Text-fig. 3F). Mean tooth width is 4.0 mm. The enamelled buccal face of each tooth is ornamented by a strong median carina. The margins of the crown are highly denticulate, but the denticles are not supported by marginal (i.e. secondary) ridges.

By contrast, teeth within the dentary are considerably wider than those within the maxilla (Text-fig. 3G).

They are also relatively wider than dentary teeth in other hadrosaurids. Mean tooth width is 8.0 mm. Unlike other hadrosaurids (with the possible exception of *Gilmoresaurus mongoliensis* [PIN 2949/1] and *Claosaurus agilis* [YPM 1190; Carpenter *et al.* in press]), dentary teeth of *T. transylvanicus* are slightly recurved distally. The apex is acutely pointed. The lingual surface of the crown bears only a low primary ridge offset somewhat mesially and sometimes a very slight, mesially-placed secondary ridge. The margins of the crown are denticulate. For mesial denticles, each is supported by a ridge on the enamelled lingual face of the crown; distal denticles are not supported by ridges.

Axial skeleton

The axial skeleton of *T. transylvanicus* is incompletely known. The best material includes three sections of the cervical series (BMNH R3841) and two partial sacra (BMNH R4911, R4915) that Nopcsa (1928) referred to this species. Additional isolated vertebral material is also known. Those that have been described include BMNH R3809, R3842, and R4973 (Nopcsa 1928). All vertebrae are preserved with the neural arches securely fused to the centra. No ossified tendons or haemal spines that might have come from these axial specimens appear to be preserved at any of the Hateg localities.

Cervical vertebrae and ribs. No atlantal material is known for *T. transylvanicus*. The axis, however, is present (BMNH R3809, R3811; Text-fig. 4A). This vertebra bears a prominent, conical dens that extends from the well-butressed cranial surface of the axial centrum. Likewise, the centrum is expanded and opisthocelous. The neural spine is long, arched, and blade-like. The neural arch is well developed, surrounding an ovate (higher than wide) vertebral canal. Cranially, the dorsolaterally facing prezygapophysis is virtually flush with the sides of the neural spine. In contrast, the postzygapophysis overhangs the caudal end of the centrum. In between, the diminutive transverse process supports a small cervical rib (see below).

The next three cervicals are strongly opisthocelous (Text-fig. 4A). In cranial view, the centrum is ovate (wider than high). The neural spines are short and diminish in size caudally within this series. The prezygapophyses progressively lengthen and project laterally down the cervical series, while the postzygapophyses lengthen and sweep caudolaterally at a very wide angle. In both these conditions, *T. transylvanicus* resembles other hadrosaurids. The parapophysis is small and oriented horizontally. Ventrally, a sagittal ridge begins faintly with the third cervical and becomes most accentuated on the undersurface of the fifth cervical. Laterally-positioned ridges lie parallel to the sagittal ridge.

The cervical-dorsal transition appears to be very gradual (Text-fig. 4B). The last cervical centrum is rather stout and subcircular in cranial view. The parapophysis, found on the lateral aspect of the neural arch, is slightly developed. Only the base of the transverse process, toward the top of the neural arch, is preserved. The postzygapophysis is elevated well above the vertebral canal and the neural spine (preserved only at its base) appears to be relatively stout.

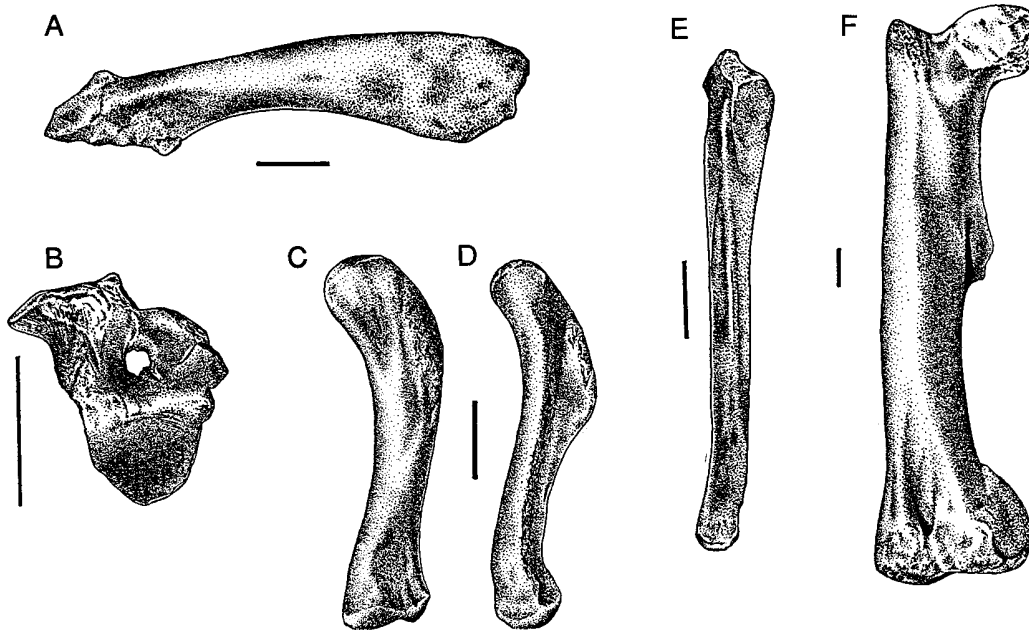
Very few cervical ribs are preserved. The atlantal rib has a single head, modestly elongate neck, and short shafts (see BMNH R3841). Successive ribs have approximately the same morphology.

Dorsal vertebrae and ribs. The number of dorsal vertebrae is unknown in *T. transylvanicus*. The first dorsal (BMNH R3842) is very similar to the last cervical (Text-fig. 4B). The centrum is slightly opisthocelous cranially to virtually platycoelous caudally. The parapophysis is strongly developed at the base of the neural arch. Like the last cervical, the transverse process extends from near the top of the neural arch, immediately beneath the prezygapophysis. Although dorsally incomplete, the neural spine appears to be of modest size, comparable to that in some hadrosaurids (e.g. *Gryposaurus notabilis*, *Edmontosaurus regalis*).

Dorsal ribs are unremarkable in their morphology (see BMNH R4911). The head is small and single, the neck is relatively long, the tubercle is large, and the shaft is shallowly curved, with a well-developed costal groove.

Sacrum and sacral ribs. Partial sacra referred to *T. transylvanicus* (BMNH R4911, R4915) indicate that the sacrum was composed of at least four vertebrae (Text-fig. 4C). Eight or nine were probably present in life. The ventral surface of these sacrals bears a prominent longitudinal ridge.

Accompanying BMNH R4911 are two sacral ribs. The more cranial articulates principally with the first preserved centrum, as well as with the cranial surface of the base of the second rib. The latter articulates solely with the side of the second centrum. Both articulate with each other at their lateral extremities. The space between these sacral ribs forms one of the sacral foramina. Isolated sacral ribs that probably pertain to *T. transylvanicus* are in the FGGUB collections (FGGUB [24], 1051).



TEXT-FIG. 5. *Telmatosaurus transsylvanicus*. A, left scapula (FGGUB [4]) in lateral view. B, fragmentary right coracoid (BMNH R3843) in lateral view. C–D, left humerus (MAFI Ob.3126) in medial and cranial views (after Weishampel *et al.* 1991). E, right ulna (MAFA Ob.3124) in lateral view. F, right femur (MAFI v.10338) in cranial view (after Weishampel *et al.* 1991). Scale = 50 mm.

Caudal vertebrae. The full complement of caudals of *T. transsylvanicus* is not presently known, but probably ranged upwards of fifty vertebrae. Isolated caudals are known from several regions of the tail (BMNH R3841, R3842, R4915, R4973; Text-fig. 4b). Proximal vertebrae are short and cylindrical, with circular intervertebral articulations. Each vertebra bears a modest neural spine that is caudodorsally upturned, much as in *Gryposaurus notabilis* and species of *Iguanodon*. The zygapophyses are oriented nearly vertically. The transverse process extends from the base of the neural arch. Ventrally, the proximal and distal aspects of the centrum bear facets for the haemal spines.

More distally, caudal vertebrae are spindle-shaped, with reduced zygapophyses and short neural spines. The ventral surface is dominated by proximal and distal facets for haemal spines and a groove that extends longitudinally between these facets.

Appendicular skeleton

The appendicular skeleton of *T. transsylvanicus* is partly known. Of the forelimb, the scapula, coracoid, humerus, and ulna are best preserved. Sternal bones, radius, and elements of the manus have not so far been recovered from the Hațeg Basin. Of the hindlimb, only the femur, tibia, and isolated metatarsals and phalanges are known (MAFI records indicate the presence of an ischium in their collections (MAFA 3125), but this specimen was destroyed in 1938). An ischium referred to *Telmatosaurus* sp. by Brinkmann (1984) is known from Upper Cretaceous beds of northeastern Spain, but, because of its provenance, will not be part of the present description. The appendicular material from the Hațeg Basin is sufficiently well preserved not only for good morphological description (including myologic interpretation; see Norman 1986) but also appropriate phylogenetic assessment.

Scapula. Known only from FGGUB [4] (Text-fig. 5A), the scapula of *T. transsylvanicus* is long and curved caudodorsally. Immediately above the glenoid region (not preserved), the blade expands slightly so that the craniodorsal and caudoventral borders diverge toward the vertebral border. Along the craniodorsal border, a

rounded acromial process is found in front of the glenoid region. The rostral side of the glenoid may accommodate the insertion of *m. trapezius*, while the caudal aspect is the origin of *m. deltoideus clavicularis*.

Coracoid. A single, partial coracoid (BMNH R3843; Text-fig. 5B) preserves the glenoid facet and a large coracoid foramen that is removed from the scapular junction by approximately 30 mm. Immediately ventral to the glenoid facet, there is a striated scar for the insertion of *m. costocoracoideus*. More ventral yet to this position, another scar marks the origins of *mm. coracobrachialis ventralis* and *triceps longus caudalis*.

Humerus. The humerus (MAFI Ob.3126; BMNH R3842, R3845, R3847) is somewhat gracile in form (Text-fig. 5C–D). The relatively large humeral head is slightly medially and caudally displaced relative to the longitudinal axis of the element. The flattened shoulder medial to the humeral head bears a prominent scar for *m. deltoideus scapularis*. The low, rounded deltopectoral crest merges imperceptibly with the main body of the humerus at midshaft level, similar to the condition found in *Camptosaurus dispar*, species of *Iguanodon*, and *Ouranosaurus nigeriensis*. The cranial margin of the deltopectoral process is not medially reflected as in such hypsilophodontids as *Orodromeus makelai* and *Hypsilophodon foxii*. The *m. deltoideus clavicularis* scar is strongly developed on the lateral surface of the deltopectoral crest, while the *m. pectoralis* scar is found on the medial surface. On the caudal aspect of the humerus, at the level of the deltopectoral crest, is an ovate scar for *mm. latissimus dorsi* and *teres major*. Beneath this region, the shaft is relatively narrow and straight. The distal humerus consists of a tear-drop-shaped ulnar condyle and a somewhat narrower radial condyle. The ulnar condyle is much larger and more ventrally placed than the radial condyle. Above the ulnar condyle, the medial epicondyle bears a supracondylar ridge that continues half-way up the humeral shaft and presumably served for the origin of the lower fibres of *m. triceps brevis intermedius*.

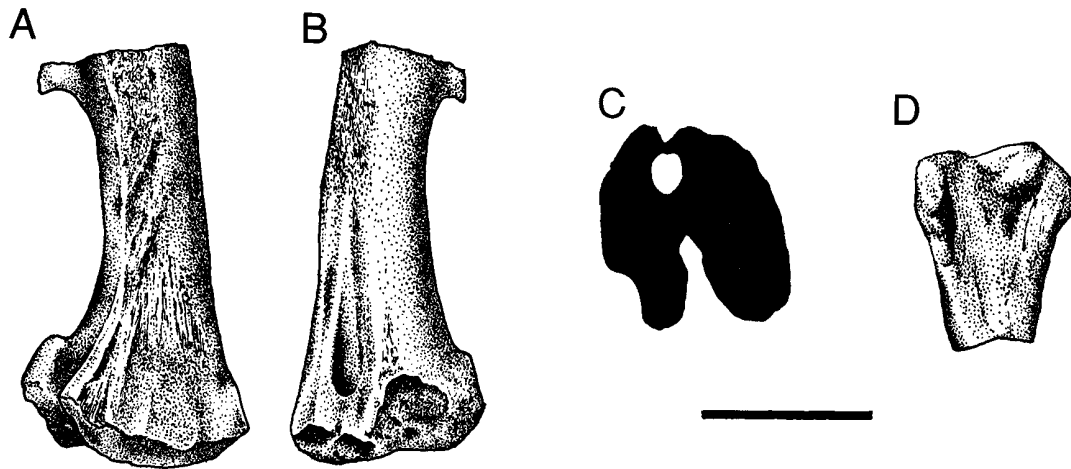
Ulna. The ulna (MAFI Ob.3124, Ob.4212; FGGUB 1078; Text-fig. 5E) is long, narrow, and relatively straight in craniocaudal views. Only in lateral view is there a slight caudal deviation of the distal ulna. The proximal head is formed into a triangular articular surface for the ulnar condyle of the humerus. The radial fossa is large and the olecranon process is moderately developed.

The lateral aspect of the ulna is raised into a relatively narrow interosseous border. Muscle scars are not particularly well developed. There appears to be a *m. pronator quadratus* scar on the proximal half and a scar for the ulnar head of *m. flexor digitorum longus* more distally on the lateral aspect of the ulnar shaft. Finally, the insertion of *m. flexor ulnaris* extends the length of the shaft on the medial aspect of the ulna. Distally, the ulna ends in a bluntly rounded articular surface. Laterally, it is flattened to accommodate the distal radius.

Femur. The femur (MJH 66; MAFI Ob.3128, v.10338; BMNH R3846, R4914, R11539; Text-fig. 5F) is slightly laterally bowed. The head is large, globose, and set on a stout neck angled approximately 145° to the long axis of the femoral shaft. More lateral, the greater and lesser trochanters are separated by a vertical cleft. The craniomedial surface of the greater trochanter probably marks the insertion of *mm. iliotrochantericus II et III*, while a rugose area on the caudal aspect marks the insertion of *mm. ischiotrochantericus* and *iliotrochantericus I*. On the lateral aspect of the lesser trochanter and possibly continuing down the shaft to the level of the lateral condyle is a scar for the insertion of *m. iliofemoralis*.

The well-developed fourth trochanter crosses the caudomedial aspect of the shaft. In this position, it is situated 45 per cent of the length of the femur from the top of the greater trochanter. A moderately developed fossa on the medial surface of the fourth trochanter probably marks the insertion of *m. caudifemoralis longus*, with the cranial margin of the fossa forming the insertion site of *m. puboischiofemoralis internus I*. The caudomedial edge of the fourth trochanter marks the insertion of *m. caudifemoralis brevis*. The remainder of the femoral shaft bears several additional muscle scars, among them the origin of *m. femorotibialis internus* on the craniomedial aspect of the femoral shaft adjacent and ventral to the fourth trochanter. This site may reach as high as the femoral neck and as ventral as a few centimetres above the medial epicondyle. More lateral, the long and narrow scar for *m. femorotibialis externus* is found between the fourth trochanter and the scar for *m. iliofemoralis*. Finally, the indistinct scar for *m. adductores* can be plausibly identified as an ovate region on the caudal aspect of the femur distal to the fourth trochanter and proximal to the femoral condyles.

The distal condyles are large and face slightly medially. The medial condyle is the larger of the two, while the lateral condyle bears a narrow condylid process (*sensu* Forster 1990). Presumably the insertion tendon of *m. iliofibularis* ran in the large groove that forms the lateral face of this condylid. Each distal condyle is shallowly convex, although both extend caudally for a considerable distance. In caudal view, there is a wide intercondylar groove between them. Cranially, the distal condyles meet to form an extensor 'tunnel' that surrounds the insertion tendon of *mm. iliotibiales* on its way to the cnemial crest of the tibia.



TEXT-FIG. 6. *Telmatosaurus transsylvanicus*. A-C, right distal femur of a hatchling (FGGUB 248) in lateral, cranial, and ventral views respectively. D, left proximal tibia of a hatchling (FGGUB 250) in lateral view. Scale = 10 mm.

In addition to these adult femora, two partial hatchling femora referable to *T. transsylvanicus* have been recently discovered in association with relatively complete eggs (Grigorescu *et al.* 1990; Weishampel *et al.* 1991). Both specimens, comprising distal ends, have a very porous, striated surface texture. FGGUB 248 (Text-fig. 6A-C), a 26.5 mm long fragment of the right femur, preserves the majority of the distal shaft from the base of the fourth trochanter to the distal condyles. From what can be seen, the fourth trochanter extends 3.5 mm from the shaft and is slightly pendent at its tip. Like adult femora, the distal condyles extend cranially beyond the shaft to enclose the cranial intercondylar groove. The caudal intercondylar groove is very deep and there is a moderately-developed condylid on the lateral condyle. It is very likely that the incomplete nature of the distal end is due to the immaturity of the element; embryonic and hatchling hadrosaurids have a very spongy endochondral femoral metaphysis (Horner and Weishampel 1988). FGGUB 249, a smaller femoral fragment, is less well preserved than FGGUB 248. It includes the distal shaft as well as proximal portions of the condyles. Both cranial and caudal intercondylar grooves are relatively deep.

Tibia. The tibia of *T. transsylvanicus* is known only from isolated fragments (MAFI Ob.3129; MNMB v.60/1708, v.60/1709). Proximally, the head is expanded, presenting a transversely flat and slightly convex craniocaudally condylar surface for the femur. The cnemial crest is relatively small and faces slightly laterally, where it surrounds the proximal fibula. More distally, the tibial shaft is relatively straight and typically twisted about its long axis.

The lateral malleolus is missing in MAFI Ob.3129, but it apparently articulated with the fibula, much like the condition in *Iguanodon atherfieldensis* and other ornithopods (Norman 1986). Ventrally, the articular surface for the astragalus is transversely expanded and rounded. The medial limit of the distal tibia is formed into a well-developed malleolus that projects well beyond the shaft.

Like the femora, hatchling-size tibial material (again associated with eggs) is also known for *T. transsylvanicus* (FGGUB 250; Text-fig. 6D). Surface texture of the specimen is striated. The relatively flat proximal end of the tibia is craniocaudally expanded. The subequal medial and lateral condyles are well developed, overhanging slightly the caudal aspect of the tibial shaft. The fibula facet is set in from the lateral surface of the cnemial crest. The latter would have wrapped slightly around the cranial aspect of the fibula.

Metatarsus and phalanges. Several isolated metatarsals (BMNH R4913, R4914; MAFI Ob.3120, Ob.3121, Ob.3122; FGGUB [11], [15]) are represented among *T. transsylvanicus* material. These pertain to metatarsals II, III, and IV. Metatarsal II (MAFI Ob.3121) is a relatively stout element, with a transversely compressed, flat proximal end. Proximally, the cranial margin of metatarsal II overhangs the more distal shaft. The shaft itself is relatively robust and laterally compressed, curving forward and slightly lateral to form the expanded distal articulation. The lateral surface of the shaft presents a broad flat surface for articulation with the medial

surface of metatarsal III. The distal condyles are separated by a modest ginglymus. The slightly more distally positioned medial condyle gives a medial deviation to the long axis of digit II.

Metatarsal III is the largest and most symmetrical of the metatarsals (MAFI Ob.3120, Ob.3122; FGGUB [15]; BMNH R4913). The proximal end is flat and expanded craniocaudally. The broad, flat surface dominating the medial aspect of metatarsal III forms the articulation with metatarsal II. The rugose lateral surface articulates with metatarsal IV. The shaft is relatively narrow throughout its length, culminating in expanded distal condyles, again separated by a ginglymus. The medial condyle is slightly smaller and less distally prolonged than the lateral condyle.

The rounded proximal end of metatarsal IV (FGGUB [11]; MAFI Ob.3120) is the least expanded of the *T. transsylvanicus* metatarsal elements. The slightly excavated medial aspect of the proximal end articulates with metatarsal III. The distal half of the round shaft curves laterally to form an expanded condyle that is only slightly separated into medial and lateral halves by a faint ginglymus.

The few phalanges referred to *T. transsylvanicus* consist only of isolated material. FGGUB 1033 comprises several phalanges. One, a stout element with an expanded distal condylar region, appears to be the first phalanx of digit III. Another, probably the first phalanx of digit II, is relatively long, with a modest, asymmetrically expanded distal end.

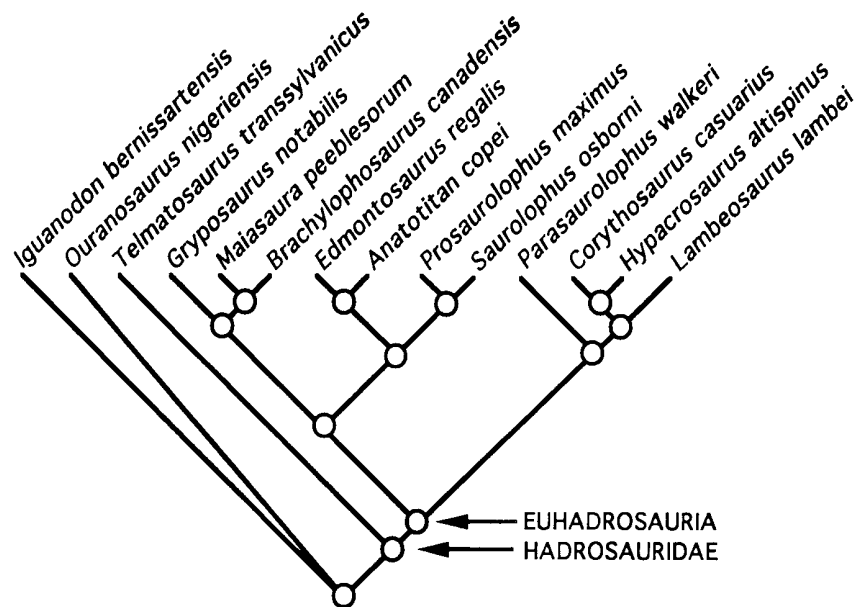
SYSTEMATIC ANALYSIS

Hadrosauridae presently comprises nearly twenty-five genera and forty species, mostly from the Western Interior of North America and central and eastern Asia, with other, rarer forms from Europe and South America (Weishampel 1990; Weishampel and Horner 1990). In order to understand their phylogenetic relationships (particularly with regard to *T. transsylvanicus*), we undertook a preliminary numerical cladistic analysis of these taxa using Phylogenetic Analysis Using Parsimony (PAUP-2.4; Swofford 1985). This analysis is based on 12 hadrosaurid species and 37 cranial, dental, and postcranial characters. *Ouranosaurus nigeriensis*, *Iguanodon atherfieldensis*, *I. bernissartensis*, and *I. lakotaensis* were used for outgroup comparisons.

The character/taxon matrix for these iguanodontians was compiled from a variety of sources, among them original observations, as well as literature sources (Serenio 1986; Horner 1990; Norman 1990; Norman and Weishampel 1990; Weishampel and Horner 1990). Those characters used in the present analyses were chosen to best reflect the relative completeness of *T. transsylvanicus*. In addition, autapomorphic features were excluded from these analyses. The resulting character/taxon matrix is largely complete (Table 1; only 1.7 per cent missing). These data were analysed using the Branch-and-Bound option of PAUP to retrieve the most parsimonious tree from the data at hand. In addition, the Accelerated Transformation and Delayed Transformation

TABLE 1. Character taxon data matrix.

OUTGROUP	000000000 000000000 000000000 0000000
<i>Iguanodon</i>	000000000 000000000 000000000 1000000
<i>Ouranosaurus</i>	100000010 000010000 001000000 0001000
<i>Telmatosaurus</i>	000000000 000110000 1000011100 1110100
<i>Gryposaurus</i>	1110101000 0000101000 1100111111 1110101
<i>Maiasaura</i>	1110001010 0001101101 1100111111 1110101
<i>Brachylophosaurus</i>	1110101010 0001101101 1100111111 1110101
<i>Edmontosaurus</i>	1110101000 001010000 1100111111 1110101
<i>Anatosaurus</i>	1110101000 001010000 1100111111 1110101
<i>Prosaurolophus</i>	1110101100 000010000 1100111111 1110101
<i>Saurolophus</i>	1110101100 000010000 1100111111 1110101
<i>Parasaurolophus</i>	1101019001 0000110011 1111111111 0111111
<i>Corythosaurus</i>	1101019001 1100110011 1111111111 0111111
<i>Hypacrosaurus</i>	1101019001 1100110011 1111111111 0111111
<i>Lambeosaurus</i>	1101019001 0100110011 1111111111 0111111



TEXT-FIG. 7. Cladogram of iguanodontoid taxa indicating the relationship of *Telmatosaurus transsylvanicus*, based on a single 44-step most-parsimonious tree with a consistency index of 0.841.

options were separately used to evaluate the level at which reversals and convergences accrued within the tree.

Analyses of the complete data matrix result in a single 44-step tree with a consistency index of 0.841 (Text-fig. 7).

On the basis of this analysis, Hadrosauridae constitutes a monophyletic clade, diagnosed on the following synapomorphies (numbers appearing in square brackets refer to characters in Appendix 1).

1. Elevation of the dorsal process of the maxilla, with concomitant migration of the antorbital fenestra onto the dorsal surface of the maxilla [20]
2. Absence of a paraquadratic foramen [21]
3. Angular positioned on the medial surface of the mandible [26]
4. Absence of surangular foramen [27]
5. Narrow maxillary teeth [28]
6. Three or more dentary teeth per tooth position [32]
7. Reduced dorsal margin of the scapular blade [35]

T. transsylvanicus possesses all of these characters and is thus an unambiguous member of the hadrosaurid clade (Weishampel and Horner 1990). However, this species lacks a number of synapomorphies that diagnose remaining members of Hadrosauridae, as follows.

1. Absence of a denticulate oral margin of the premaxilla [2]
2. Narrow mandibular condyle of the quadrate [22]
3. Narrow dentary teeth [29]
4. Large single carina on dentary teeth [30]
5. Angular deltopectoral crest [37]

A transversely expanded rostrum (character 1) and a mandibular diastema (character 25) may constitute further synapomorphies of this clade using the DELTRAN option of PAUP (convergently evolved in *Ouranosaurus nigeriensis*). However, when synapomorphies are accelerated (ACCTRAN option), these features are positioned as a synapomorphy of Hadrosauroidea (*sensu* Sereno 1986), with a reversal in *T. transsylvanicus*. As a consequence of this conflict, it is at present impossible to assess the significance of rostral expansion and mandibular diastema among these taxa.

The hadrosaurid clade united by these synapomorphies, here termed Euhadrosauria, consists of the traditional grouping of lambeosaurines and hadrosaurines (Weishampel and Horner 1990).

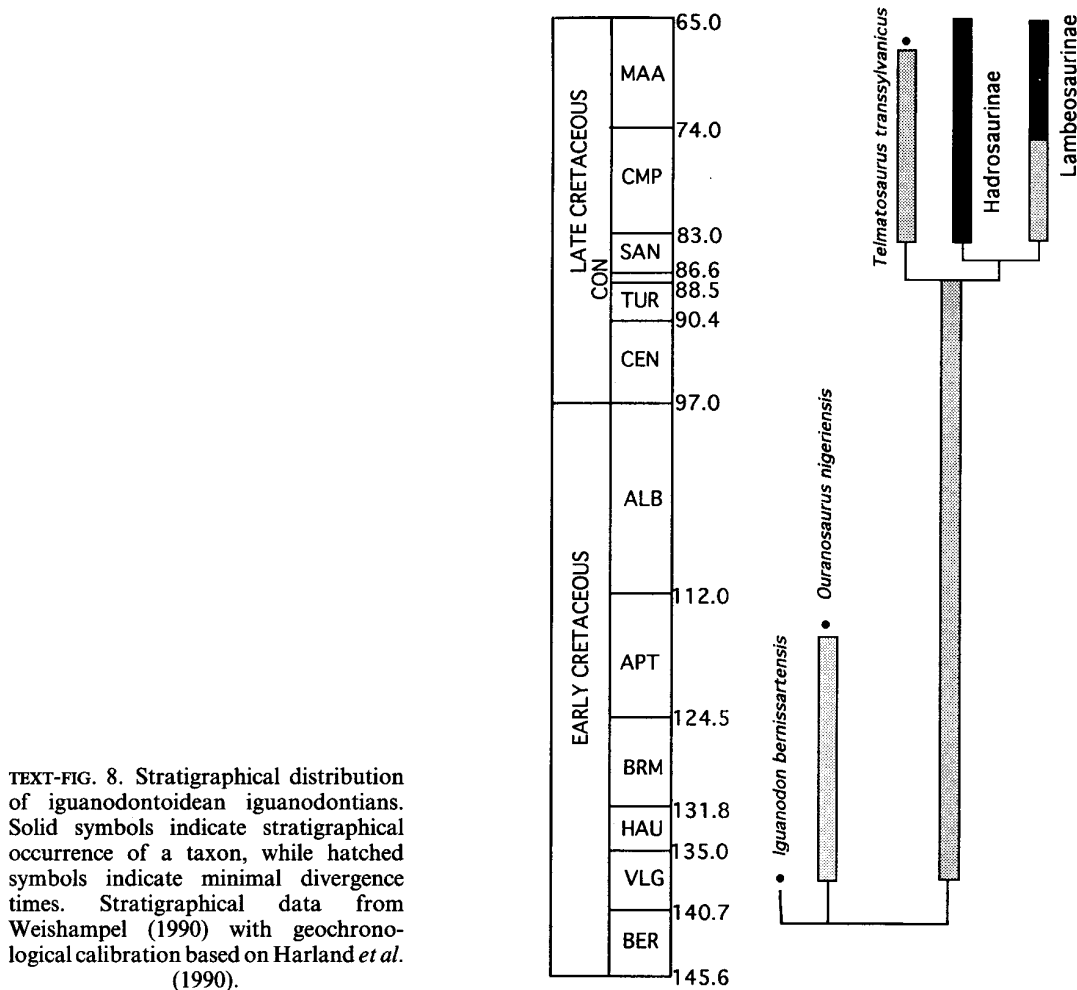
T. transsylvanicus itself possesses a number of autapomorphies: reduced body size, large caudal ectopterygoidal shelf, isosceles triangle-shaped rostral process of the jugal, relatively long post-metotic braincase, relatively large basiptyergoid processes, large scar for *m. protractor pterygoideus* on the lateral aspect of the basisphenoid, well-developed channel for the palatine branch of the facial nerve that also accommodated the median cerebral vein, and bowed femur. Reversal of rostral expansion and absence of a diastema between the prementary and dentary dentition may also constitute autapomorphies of *T. transsylvanicus*.

DISCUSSION

As originally noted by Nopcsa (1934; see also Weishampel *et al.* 1991), virtually all of the animals from the Upper Cretaceous sites of Transylvania, including *T. transsylvanicus*, were considerably smaller than their relatives elsewhere. That they were not juveniles or subadults at the time of their death is indicated by the degree of fusion of the braincase and vertebrae. As an adult, *T. transsylvanicus* was probably no more than approximately 5 m in length and weighed in excess of 500 kg, which is at most 10 per cent of an average adult of other hadrosaurid species. Other less well known dinosaur taxa from the Hațeg region are equally small compared to relatives elsewhere. Of relevance here is Nopcsa's (1923, 1934) identification of the Hațeg region as one of many islands comprising a trans-European archipelago in the Late Cretaceous. Armed with this knowledge, Nopcsa regarded small body size among these Transylvanian dinosaurs as examples of dwarfing on islands. Dwarfism is relatively common on islands (Case 1978; Heany 1978; Marshall and Corruccini 1978; Ford 1980; Pregill 1986) and it probably should not be unexpected among taxa found on the 'Hațeg island'. Such dwarfism in *T. transsylvanicus* may involve heterochronic alterations of growth processes. Accordingly, the miniaturization of the maxillary dentition and the evolution of a dental battery in *T. transsylvanicus*, and perhaps all hadrosaurids, may owe their development to progenetic paedomorphosis (see McKinney 1988 for use of terms).

Despite the possibility of dwarfism, *T. transsylvanicus* appears to be little different ecologically from other, larger iguanodontoidean iguanodontians. For example, the serrate oral margin, large adductor muscle mass, and pleurokinetic construction of the skull are all plesiomorphic within this nexus of iguanodontian history and hence suggest that *T. transsylvanicus* had feeding habits similar to more basal iguanodontians such as *Ouranosaurus nigeriensis* and species of *Iguanodon*. In this way, *T. transsylvanicus* was probably little different from these animals in either procuring or processing food. Transverse chewing motion between upper and lower teeth appears to have been achieved by slight lateral rotation of the maxillae (Norman 1984; see also Weishampel 1984; Norman and Weishampel 1985).

In contrast, other features found in *T. transsylvanicus* appear to have their evolutionary origin (i.e. are apomorphic) basally in Hadrosauridae. These include elevation of the dorsal process of the maxilla, miniaturization of the maxillary dentition, and the development of a battery of dentary teeth. That these features appear to have evolved together suggests a shift in feeding among hadrosaurids relative to outgroup taxa. Such changes involve altering the behaviour of some of the links within the kinematic framework of the skull, increasing the complexity of the maxillary occlusal surface, and creating an entirely new organization of tooth replacement, ultimately producing a new construction for the masticatory system.



For *T. transsylvanicus* itself, several unique features suggest that its feeding mechanics may have been different from those of other iguanodontoideans. For example, the size of the scar for *m. protractor pterygoideus*, coupled with the relatively large basipterygoid processes in *T. transsylvanicus* may indicate that the basicranial-constrictor dorsalis musculoskeletal system (the maxillary-return mechanism in pleurokinesis; Norman 1984; Weishampel 1984) was emphasized to a greater degree than in other taxa.

It is very difficult to assess the locomotor organization of *T. transsylvanicus*, principally because of the lack of appropriate portions of the limbs. However, there is very little to suggest that these regions differed much from those of other iguanodontoideans. The fore and hindlimb are very similar to those of *Iguanodon* and *Ouranosaurus*. Where they differ – in the reduced nature of the dorsal scapular margin, and the parallel borders of the scapular blade (both apomorphic for Hadrosauridae) – these features are difficult to interpret functionally. The slightly bowed femur of *T. transsylvanicus* may indicate different hindlimb kinematics from that in other hadrosaurids, both young and adult. Conversely, it may be due to reduced peak stresses operating during locomotion in a relatively small animal; bone curvature of the kind seen in *T. transsylvanicus* is less constrained

at smaller body size, particularly when the predictability of loads is considered (Biewener 1983; Bertram and Biewener 1988). Should the latter be true, *T. transsylvanicus* may have walked and run no differently from larger hadrosaurid species.

Whatever the functional qualities of *T. transsylvanicus* relative to other iguanodontians, the basal phylogenetic position of this species within Hadrosauridae (Text-fig. 7) and late stratigraphical distribution of this species (Text-fig. 8) appear at face value to be highly discordant (see Weishampel *et al.* 1991). The discordance implied by basal species known only from late within the history of a clade can be studied through the use of minimal divergence times (MDTs; see Norell 1987, 1992; Gauthier *et al.* 1989; Benton 1990; Sereno 1991; Weishampel 1991; Weishampel and Heinrich 1992). MDTs are based initially on the sibling relationships among taxa. These relationships establish phylogenetic continuity from common ancestor to each terminal taxon. Because the common ancestor of two sister taxa can be no younger than each sister taxon, the oldest stratigraphical occurrence of each terminal taxon – and subsequently each node – sets the youngest limit for the other sister taxon. The difference in ages between sister taxa is thus a measure of the minimal divergence time of the younger of the two taxa. Consequently, species-level MDTs are a measure of the completeness of the fossil record from a phylogenetic perspective.

Using MDTs to understand the evolutionary and temporal distribution of *T. transsylvanicus* requires an understanding of the biostratigraphy of remaining hadrosaurids. The oldest age for diagnosable euhadrosaurian taxa is at least ?Early Campanian (the age of *Lophorhothon atopus*). However, this earliest appearance of Euhadrosauria may extend to the Turonian, if Rozhdestvensky (1968) is correct in his assessment of the stratigraphic distribution of Kazakhstan hadrosaurids. The sister-group relationship between *T. transsylvanicus* and Euhadrosauria thus requires that the common ancestor of both taxa is no younger than the older of the two taxa. This relationship implies MDTs of at least 18 million years (and possibly as much as 23 million years) between the first appearance of euhadrosaurian taxa and the appearance of *T. transsylvanicus*. These MDT values are the highest for Hadrosauridae, but near the mean for those available for Dinosauria (Weishampel unpublished data).

High MDT values assuredly mean that some number of species-level taxa yet to be discovered are required to maintain this MDT-based phylogenetic continuity (Weishampel 1991). For *T. transsylvanicus*, the reason that this portion of hadrosaurid history is so poorly known may be a combination of the geographical and depositional setting of these same undiscovered taxa. Given the trans-European archipelago of the Late Cretaceous, we previously suggested that the restricted distribution of *T. transsylvanicus* may have been the result of island hopping, itself a consequence of the dispersal abilities of the animal (Weishampel *et al.* 1991). Our conclusions were based on the geographical distribution of iguanodontoidean iguanodontians as indicated here (i.e. species of *Iguanodon*, *Ouranosaurus nigeriensis*, Hadrosauridae including *T. transsylvanicus*) and the geological history of Europe throughout the Cretaceous. It is clear, however, that whatever the explanation (e.g. vicariance, dispersal) for the geographical distribution of *T. transsylvanicus*, such explanations ultimately depend on an adequate sampling – perhaps as expressed as MDTs – of taxa from the fossil record. In this case, it is very likely that the patchiness of islands in time and space limit our ability to sample much of the line culminating in *T. transsylvanicus*.

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- question about the actual date of publication of this paper. Nopcsa personally presented the results of his study on *Limnosaurus* (= *Telmatosaurus*) *transylvanicus* to the Vienna Academy of Science on 21 June 1899 [the name *Limnosaurus* was erected – as a *nomen nudum* – in Nopcsa, 1898, *Jegyzetek Hátszeg vidékének geológiájához. Földtani Közlemény*, **29**, 332–335], but the publication of this work appears not to have been until 1900 [see Brinkmann 1988]).
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APPENDIX 1

Cranial characters

1. Lateral expansion of the rostrum. In Ornithopoda ancestrally, the rostrum is relatively narrow. This primitive condition is retained among hadrosaurids in *Telmatosaurus* and Lambeosaurinae. By contrast, the rostrum is considerably more expanded in *Gryposaurus*, *Maiasaura*, *Brachylophosaurus*, *Edmontosaurus*, *Anatotitan*, *Prosaurolophus*, and *Saurolophus* among hadrosaurids, and *Ouranosaurus*. Such a distribution renders character 1 ambiguous with respect to the taxa under consideration. It may either be a synapomorphy of Hadrosaurinae, convergently evolved in *Ouranosaurus* when using the DELTRAN option, or it may constitute a synapomorphy of Hadrosauroida (i.e. *Ouranosaurus* + Hadrosauridae; Sereno 1986) using the ACCTRAN option.
2. Absence of a denticulate oral margin of the premaxilla and predentary. Primitively for Ankylopollexia, the oral margin of the premaxilla and predentary is strongly denticulate (see *Camptosaurus*, *Iguanodon*, *Ouranosaurus*; Weishampel and Heinrich 1992). *Telmatosaurus* also retains this denticulate oral margin, at least for the premaxilla (predentary is unknown). In contrast, the oral margins of the premaxilla and predentary are not overtly denticulate in lambeosaurine and hadrosaurine taxa (Weishampel and Horner 1990). Given such a character distribution, character 2 is best interpreted as a synapomorphy of Euhadrosauria.
3. Reflected premaxillary lip. Primitively in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*, the premaxilla extends laterally without other alterations to the margins of the narial fossa. This primitive condition is also retained in lambeosaurine taxa. In contrast, the lateral margins of the premaxilla fold dorsally to form a prominent lip that mark the ventral wall of the narial fossa in *Gryposaurus*, *Maiasaura*, *Brachylophosaurus*, *Edmontosaurus*, *Anatotitan*, *Saurolophus*, and *Prosaurolophus*. Horner (1990) argued that this feature constitutes a synapomorphy of Hadrosauria (*Iguanodon* + non-lambeosaurine hadrosaurs). However, given that the lateral margin of the premaxilla does not form an appreciable reflected lip in *Iguanodon* and given that *Telmatosaurus* (also without a lip) is interposed between this more basal form and other hadrosaurid taxa, character 3 is best interpreted as a synapomorphy for Hadrosaurinae.
4. Absence of premaxillary foramina. Premaxillary foramina, which form the openings for a canal between the narial fossa and palatal surface of the premaxilla, are present ancestrally in Euornithopoda (Weishampel and Heinrich 1992). Compared with this primitive condition, the premaxilla lacks these basally in *Corythosaurus*, *Lambeosaurus*, *Parasaurolophus*, and *Hypacrosaurus*. Loss of premaxillary foramina is consequently identified as a synapomorphy of Lambeosaurinae. Thus, this evaluation supports the interpretation of Horner (1990; *sensu* Lambeosauridae).

5. Enlarged external naris. Primitively for Ankylopollexia, the external naris is little more than 20 per cent basal skull length. This ancestral condition is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, *Maiasaura*, and lambeosaurine taxa. In contrast, the external naris is relatively large (up to 40 per cent basal skull length) in *Gryposaurus*, *Brachylophosaurus*, *Prosaurolophus*, *Saurolophus*, *Edmontosaurus*, and *Anatotitan*. In contrast to Sereno (1986), who regarded enlarged external nares as a synapomorphy of Iguanodontoidea (= *Iguanodon* + *Ouranosaurus* + Hadrosauridae), our analyses place character 5 as a synapomorphy of Hadrosaurinae, in agreement with Horner (1990; *sensu* Hadrosauridae). The relatively small external naris in *Maiasaura* then constitutes a reversal within Hadrosaurinae.
6. External naris surrounded by the premaxilla. In Iguanodontia ancestrally, the external naris is surrounded on its rostral, and ventral sides by the premaxilla, while its dorsal and caudal margins are formed by the nasal. This primitive condition is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Hadrosaurinae. In contrast, the external naris of *Parasaurolophus*, *Corythosaurus*, *Hypacrosaurus*, and *Lambeosaurus* is completely surrounded by the premaxilla. Although hierarchical levels differ, the present study supports Horner's (1990) identification of this character as a synapomorphy for Lambeosaurinae.
7. Circumnarial depression extending onto the nasal. The external surface of the nasal is relatively flat (i.e. not marked by a fossa or excavation) primitively in Ornithischia. The feature is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Lambeosaurinae. *Gryposaurus*, *Brachylophosaurus*, *Maiasaura*, *Prosaurolophus*, *Saurolophus*, *Anatotitan*, and *Edmontosaurus* differ from this ancestral condition; the nasal bears a faint to well-developed circumnarial depression immediately caudal to the external nares. Because of the migration of the nasal cavity in lambeosaurines to a supracranial position, a circumnarial depression is considered missing in this taxon. With such a character distribution (see also Horner 1990), the hadrosaurine clade is united by character 7.
8. Narrow solid crest. Ancestrally in Ornithischia (and beyond), the skull roof is relatively flat, unadorned by any cranial excrescence. This condition is retained through *Iguanodon* and basally in Hadrosauridae (see *Telmatosaurus*). In contrast, the caudal aspect of the nasals and adjacent frontals are raised into a relatively narrow, low-lying crest in *Prosaurolophus* and *Saurolophus*. Consequently, character 8 is interpreted as a synapomorphy uniting these two taxa (i.e. saurolophs; Weishampel and Horner 1990).
9. Broad solid crest. As indicated above, the supraorbital region among iguanodontians is primitively flat. In contrast, the broad, solid crest, seen in *Maiasaura* and *Brachylophosaurus* is considered derived, thus constituting a synapomorphy of this small clade of maiasaurs (Weishampel and Horner 1990). The crest of *Ouranosaurus* then constitutes a case of convergence.
10. Modified nasal cavity. In at least Ornithischia ancestrally, the nasal cavity (vestibule, cavum nasi proprium, nasopharyngeal duct) is formed rostral to the orbital region by the facial skeleton. This condition is found throughout Iguanodontia, including *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Hadrosaurinae. The derived condition, in which the cavum nasi proprium is positioned above the orbit and skull roof, is found in *Lambeosaurus*, *Corythosaurus*, *Parasaurolophus*, and *Hypacrosaurus*. As has long been known, modification of the nasal cavity to a supraorbital position uniquely unites Lambeosaurinae.
11. Nasal forming half of the crest. Polarizing features of the crest in Lambeosaurinae is somewhat difficult, given that the sister taxon to the group lacks a hollow crest. However, given what is known about the ontogenetic development of the crest (Dodson 1975; Hopson 1975; Weishampel 1981), it may be possible to infer some aspects of crest polarity. Thus ancestrally the crest of lambeosaurines appears to be formed principally from bones surrounding the vestibule (premaxillae), with the nasals contributing only a small portion of the crest base. A crest bearing large contributions from the nasal, especially around the cavum nasi proprium is thus considered the derived condition, seen in *Hypacrosaurus*, *Lambeosaurus*, and *Corythosaurus*. Character 11 thus constitutes a synapomorphy for the small clade consisting of these three taxa (Weishampel and Horner 1990).
12. Enlargement of the common median chamber. Using the same ontogenetic argument outlined above, the cavum nasi proprium of Lambeosaurinae is relatively small primitively within the clade. In contrast, the chamber is much enlarged in *Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*. In our analyses, character 12 stands as a synapomorphy of the clade consisting of these three taxa (Weishampel and Horner 1990).
13. Massive jugal. A relatively gracile jugal is present ancestrally in Iguanodontia, a condition retained in nearly all of the taxa under consideration here. A striking enlargement of the jugal is apomorphically present in *Edmontosaurus* and *Anatotitan*. In our analyses, character 13 constitutes a synapomorphy for the small clade of edmontosaurs (Weishampel and Horner 1990).

14. Isosceles-triangle-shaped rostral process of the jugal. In at least Iguanodontia ancestrally, the rostral end of the jugal, where it articulates with the maxilla, is roughly triangular, but asymmetric. Among the taxa under consideration here, this condition is retained in *Iguanodon*, *Ouranosaurus*, and nearly all Hadrosaurinae. In Lambeosaurinae, the rostral portion of the jugal is truncated and broadly curved (see character 16). In contrast to these conditions, the rostral end of the jugal in *Telmatosaurus*, *Maiasaura*, and *Brachylophosaurus* is nearly shaped like an isosceles triangle. This condition independently diagnoses the small clade of *Maiasaura* and *Brachylophosaurus* (maiasaurs; Weishampel and Horner 1990), while its presence in *Telmatosaurus* is considered convergent.
15. Dorsoventral expansion of the rostral end of the jugal. Primitively for at least Ornithischia, the rostral region of the jugal is relatively narrow, little larger than the area beneath the orbital rim. Among the animals under consideration here, *Iguanodon* retains this ancestral condition. The derived condition, in which the rostral aspect of the jugal is dorsoventrally expanded, is seen in *Ouranosaurus* and all hadrosaurid taxa. As Sereno (1986) originally noted, this character constitutes a synapomorphy for the clade of *Ouranosaurus* + Hadrosauridae (Hadrosauroida *sensu* Sereno 1986).
16. Truncated, rounded rostral process of the jugal. Ancestrally for Iguanodontia, the articular relationships among the jugal, maxilla, and lacrimal are such that the rostral extreme of the jugal is distinctly angular. This primitive condition is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Hadrosaurinae. The development of a truncated, rounded rostral aspect of the jugal is apomorphically found in *Parasaurolophus*, *Hypacrosaurus*, *Corythosaurus*, and *Lambeosaurus*. In our analyses, character 16 forms a synapomorphy for Lambeosaurinae.
17. Shallow caudal jugal process. Primitively, the caudal process of the jugal is relatively dorsoventrally broad among ornithischians, a condition retained throughout much of Iguanodontia (i.e. *Iguanodon*, *Ouranosaurus*, Lambeosaurinae, and the majority of Hadrosaurinae). The apomorphic acquisition of a shallow caudal process occurs in *Gryposaurus*, *Brachylophosaurus*, and *Maiasaura*. This feature thus constitutes a synapomorphy for the small clade of these taxa.
18. Scalloped ventral margin of caudal process of the jugal. Ancestrally for Iguanodontia, the caudal process of the jugal is ventrally straight to slightly convex in lateral view. Retention of this feature is found in *Iguanodon*, *Ouranosaurus*, Lambeosaurinae, and virtually all Hadrosaurinae. In contrast, a jugal with a caudal process that is ventrally concave, yielding a scalloped silhouette in lateral view, is found in *Gryposaurus*, *Brachylophosaurus*, and *Maiasaura*. Character 18 stands as a synapomorphy for this small hadrosaurine clade.
19. Maxillary shelf. Ancestrally in Iguanodontia (see Sereno 1986), the articulation between the maxilla and premaxilla is marked by a broadening of the contact surface and the development of a rostrolateral maxillary process that aids the rostromedial maxillary process in supporting the more dorsal premaxilla. Within Hadrosauridae, this condition is retained in *Telmatosaurus* and Hadrosaurinae. Unlike these animals, *Corythosaurus*, *Hypacrosaurus*, *Parasaurolophus*, and *Lambeosaurus* are known to lack the rostromedial process, instead having a medial maxillary shelf that supports the inner aspect of the maxilla-premaxilla contact. We do not believe that *Ouranosaurus* had a maxillary shelf, as did Horner (1990) who used this feature as a synapomorphy of *Ouranosaurus* + Lambeosaurinae (his Lambeosauria). Our analyses instead position character 19 as a synapomorphy for the more restricted taxon, Lambeosaurinae.
20. Elevation of the dorsal process of the maxilla. In Ornithischia primitively, the dorsal process of the maxilla is only slightly elevated. This condition is retained in *Iguanodon* and *Ouranosaurus*, among the taxa under consideration here. In contrast, the dorsal maxillary process is considerably elevated in *Telmatosaurus*, Lambeosaurinae, and Hadrosaurinae. A morphological consequence of the elevation of the dorsal maxillary process is the migration of the antorbital fenestra to take a position along the upper reaches of the premaxillary articular surface (Weishampel and Horner 1990). Given its distribution, character 20 constitutes a synapomorphy for Hadrosauridae.
21. Absence of a paraquadratic foramen. In at least Ankylopollexia ancestrally, the quadratojugal articulates with the quadrate in such a way that there is a gap between the two (paraquadratic foramen; see *Camptosaurus*, *Iguanodon*, *Ouranosaurus*). In contrast to these taxa, virtually all Hadrosaurinae, all Lambeosaurinae, and probably also *Telmatosaurus*, appear to lack a paraquadratic foramen. Character 21 consequently stands as a synapomorphy for Hadrosauridae.
22. Narrow mandibular condyle. In at least Dinosauria ancestrally, the mandibular condyle of the quadrate is transversely expanded, forming a well-developed roller joint with the mandibular glenoid. In Iguanodontia, this condition is retained in *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. In contrast, all hadrosaurine and lambeosaurine taxa under

- consideration have a relatively narrow and subhemispheric mandibular condyle. Character 22 is consequently apomorphically acquired in Euhadrosauria.
23. Short parietal. In *Iguanodon*, *Telmatosaurus*, and Hadrosaurinae, the parietal is relatively long. This condition appears to be ancestral not only for these taxa, but also for Iguanodontia in general, as it is primitively present in *Camptosaurus* and *Tenontosaurus*. In contrast, *Ouranosaurus*, *Corythosaurus*, *Lambeosaurus*, *Parasaurolophus*, and *Hypacrosaurus* have a relatively short parietal. Shortening of the parietal is seen as independent acquisitions of *Ouranosaurus* and Lambeosaurinae.
 24. Ventral margin of the foramen magnum formed of the basioccipital. Primitively in Iguanodontia, the exoccipital condyloids nearly or completely exclude the basioccipital from the margins of the foramen magnum. This condition is encountered in *Iguanodon*, *Telmatosaurus*, and Hadrosaurinae, but contrasts with that found in *Ouranosaurus* and Lambeosaurinae, in which the exoccipital condyloids are well separated medially, allowing the basioccipital to form the ventral margin of the foramen magnum. Horner (1990) interpreted the well-separated condyloid condition as primitive, which suggests that condyloid closure is apomorphic at least for Hadrosauridae. However, such polarity appears to be incorrect, rendering character 24 a synapomorphy of Lambeosaurinae, convergently attained in *Ouranosaurus*.
 25. Diastema in mandible. Ancestrally in Ornithischia, the dentary dentition begins immediately behind the caudal limits of the lateral processes of predentary. *Iguanodon* and *Telmatosaurus* retain this condition. In contrast, *Ouranosaurus*, Hadrosaurinae and Lambeosaurinae have caudally displaced dentary dentitions in which a pronounced diastema is formed between the predentary and mesialmost tooth position. Given this distribution, character 25 is ambiguous with respect to tree topology. The ACCTRAN option identifies the acquisition of a mandibular diastema as a synapomorphy of Hadrosauroidae (*sensu* Sereno 1986). This feature is then independently reversed in *Telmatosaurus*. With the DELTRAN option, character 25 becomes an autapomorphy for *Ouranosaurus* and a synapomorphy for Euhadrosauria. Without additional characters and/or taxa, it is presently impossible to discriminate among these possibilities. Thus the phylogenetic significance of a mandibular diastema remains unclear.
 26. Angular positioned on the medial surface of the mandible. The angular has a ventral and slightly lateral position ancestrally in Ornithopoda. Those taxa under consideration that retain this plesiomorphic condition include *Iguanodon* and *Ouranosaurus*. In contrast, the angular has a more medial disposition in *Telmatosaurus*, Hadrosaurinae, and Lambeosaurinae. This medial angular condition is therefore considered derived for Hadrosauridae.
 27. Absence of surangular foramen. A foramen is primitively present in the body of the surangular near the mandibular glenoid in Hypsilophodontidae and basal Iguanodontia (*Tenontosaurus*, *Dryosaurus*, *Iguanodon*, *Ouranosaurus*). In contrast, *Telmatosaurus*, Hadrosaurinae, and Lambeosaurinae lack a surangular foramen. Our analysis indicate that character 27 is apomorphically lost in Hadrosauridae.

Dental characters

28. Miniaturization of maxillary teeth. Primitively in Iguanodontia, maxillary teeth are relatively broad and few in number. For the taxa under consideration, *Iguanodon* and *Ouranosaurus* retain this plesiomorphy. However, in *Telmatosaurus*, Lambeosaurinae, and Hadrosaurinae, maxillary teeth are much reduced in size and packed into a mosaic of replacement. This miniaturization of the maxillary dentition constitutes a synapomorphy for Hadrosauridae.
29. Miniaturization of the dentary teeth. A dentary dentition composed of relatively broad teeth has a primitive distribution in Iguanodontia, a condition also retained in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. The apomorphic state, a reduction in dentary tooth size and an increase in number of dentary teeth, is seen in hadrosaurine and lambeosaurine taxa. This miniaturization of dentary teeth apomorphically diagnoses Euhadrosauria.
30. Large single carina on dentary teeth. Ancestrally in Ankylopollexia, the crowns of dentary teeth have a number of ridges that adorn their lingual surfaces, but none of these ridges is strikingly more prominent than another. This plesiomorphy is retained in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. In contrast, a strongly developed, single carina is found in lambeosaurine and hadrosaurine taxa. This distribution for character 30 allots it as a synapomorphy of Euhadrosauria.
31. Angle between the crown and root of dentary teeth less than 130°. Primitively, the angle between the crown and root of dentary teeth is relatively high, a condition retained in *Camptosaurus*, *Ouranosaurus*, *Telmatosaurus*, and Lambeosaurinae, among ankylopollexian iguanodontians. In Hadrosaurinae,

however, the angle is less than 130°. In our analyses, character 31 constitutes a synapomorphy for Hadrosaurinae, convergently evolved in *Iguanodon*.

32. Three or more dentary teeth per tooth position. Ancestrally for Ornithischia, the dentary dentition is formed of a single functional tooth and a single replacement. This condition is also seen in basal iguanodontians, among them *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Iguanodon*, and *Ouranosaurus*. In contrast, the dentary dentition of *Telmatosaurus*, Lambeosaurinae, and Hadrosaurinae consist in from three to five teeth per tooth position. Character 32 has long been identified as a synapomorphy for Hadrosauridae (Lull and Wright 1942; Ostrom 1961).

Postcranial characters

33. Groove on the ventral surface of the sacrum. In Euornithopoda, the ventral surface of the sacrum plesiomorphically bears a longitudinal ridge. This condition is retained not only in *Camptosaurus* and *Iguanodon*, but also all hadrosaurine taxa under consideration. In contrast, in *Ouranosaurus*, *Corythosaurus*, *Lambeosaurus*, *Hypacrosaurus*, and *Parasaurolophus*, the ventral surface of the sacrum is longitudinally grooved. In our analyses, character 33 stands as an autapomorphy for *Ouranosaurus* and as a synapomorphy for Lambeosaurinae (*contra* Horner 1990 who identified a ventrally ridged sacrum as a synapomorphy for his Hadrosauria).
34. Very tall neural spines. Primitively in Iguanodontia, the neural spines of the dorsal, sacral, and caudal series are of modest height. This condition is plesiomorphically retained in *Iguanodon*, *Telmatosaurus*, and Hadrosaurinae. In contrast, the neural spines are very tall in *Ouranosaurus* and Lambeosaurinae. Given this distribution, character 34 is apomorphic for Lambeosaurinae, convergently acquired in *Ouranosaurus*.
35. Reduced dorsal margin of the scapular blade. In at least Iguanodontia ancestrally, the dorsal margin of the scapular blade is expanded. This primitive condition is known to be retained in *Iguanodon* (*contra* Horner 1990) and *Ouranosaurus*. By contrast, the dorsal scapular margin is reduced relative to the midsection of the blade in *Telmatosaurus* and all hadrosaurine and lambeosaurine taxa under consideration. Thus, this character constitutes a synapomorphy for Hadrosauridae.
36. Robust humerus. Primitively in Iguanodontia, the humerus is relatively gracile, with a relatively small midshaft diameter relative to humeral length and a modestly developed deltopectoral crest. This humeral condition is found in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and hadrosaurine taxa. Compared to this ancestral condition, the humerus is much more robust (greater relative humeral diameter, larger and deeper deltopectoral crest) in *Parasaurolophus*, *Hypacrosaurus*, *Lambeosaurus*, and *Corythosaurus*. Given its taxonomic distribution, character 36 is apomorphic for Lambeosaurinae.
37. Angular deltopectoral crest. The humerus bears a well-rounded deltopectoral crest primitively in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. Compared to this ancestral condition, the ventral margin of the deltopectoral crest extends much more abruptly from the humeral shaft to give a distinctly angular profile to the crest in all known hadrosaurines and lambeosaurines. Given this distribution, our analyses mark character 37 as a synapomorphy of Euhadrosauria.