Geologie en Mijnbouw **78:** 345–356, 1999.
© 1999 *Kluwer Academic Publishers. Printed in the Netherlands.*

A primitive euhadrosaurian dinosaur from the uppermost Cretaceous of the Ager syncline (southern Pyrenees, Catalonia)

M.L. Casanovas[1], X. Pereda Suberbiola[2,4], J.V. Santafé[1] & D.B. Weishampel[3]
[1]*Institut de Paleontologia 'M. Crusafont', Escola Industrial 23, E-08201 Sabadell (Barcelona), Spain;* [2]*Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencias, Laboratorio de Paleontología, Apartado 644, E-48080 Bilbao, Spain, and Muséum National d'Histoire Naturelle, Laboratoire de Paléontologie, 8 rue Buffon, F-75005 Paris, France;* [3]*Department of Cell Biology and Anatomy, Johns Hopkins University School of Medicine, Baltimore, Maryland 21205, USA;* [4]*corresponding author*

Received 17 September 1998; accepted in revised form 15 April 1999

Key words: Hadrosauridae, Iberian peninsula, Lleida, Maastrichtian

Abstract

New hadrosaurid material is recorded from Fontllonga (Ager syncline, province of Lleida), in the Catalonian Pyrenees, comprising a dentary with part of the dental battery, recovered from Late Maastrichtian strata (Tremp Formation), close to the presumed Cretaceous/Tertiary boundary. This hadrosaurid is more derived than is *Telmatosaurus transsylvanicus* from the Haţeg Basin (Romania) , but lacks a number of features that diagnose the clade Hadrosaurinae plus Lambeosaurinae. It is attributed to the Euhadrosauria on the basis of the following synapomorphies: dentary teeth not recurved distally, narrow dentary crowns, and denticles not supported by subsidiary ridges. The phylogenetic relationships of the best-known iguanodontids and hadrosauroids are evaluated using mandibular and dentary tooth characters. On the basis of a cladistic analysis, the family of Hadrosauridae is diagnosed by more than 29 dentary tooth positions, parallel-sided vertical furrows formed by dentary alveoli, and absence of caudal secondary ridges. Within Hadrosauridae, successive sister-groups of Hadrosaurinae plus Lambeosaurinae are the Fontllonga taxon and *Telmatosaurus*. The clade Hadrosaurinae plus Lambeosaurinae is characterised mainly by a coronoid process inclined rostrally and by the absence of secondary ridges on dentary crowns. The Fontllonga find suggests the diversity of European hadrosaurids at the end of the Cretaceous to have been greater than previously thought. Moreover, the primitive character of European hadrosaurids as compared to western North American and Asian relatives may be explained in terms of geographical isolation during the Late Cretaceous.

Introduction

Hadrosaurids, or duck-billed dinosaurs, were a major component of terrestrial vertebrate faunas of Laurasia during the Late Cretaceous (Weishampel & Horner 1990). Most of the hadrosaurian material has been recovered from the Western Interior of North America and from central and eastern Asia, with other, rarer, remains from Europe and South America (Weishampel 1990). In Europe, hadrosaurids from latest Cretaceous strata have been known for over a century (Seeley 1883, Nopcsa 1900). Hadrosaurian sites are located in Crimea, Transylvania, Bavaria, Limburg, Liège, Languedoc, Gascony, Catalonia and Valencia (see Brinkmann 1988 and references therein, Le Loeuff et al. 1993, Weishampel et al. 1993, Santafé & Casanovas 1993, Wellnhofer 1994, Laurent et al. 1997, Mulder et al. 1997, Jagt et al. 1998, Company et al. 1998).

The first record of hadrosaurids in the Iberian peninsula dates from 1984 (Brinkmann 1984). Since this time, many discoveries have been made in the Maastrichtian of Catalonia; they have considerably improved our knowledge of hadrosaurian faunas of southwestern Europe (Casanovas 1992; Casanovas et al. 1985, 1986, 1987, 1993, 1995, 1997, 1998, 1999).

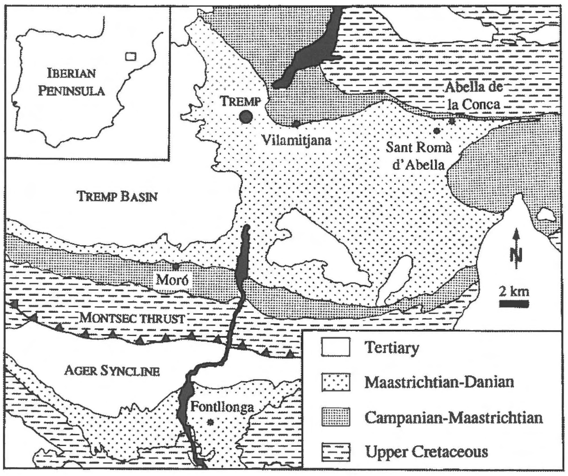

Figure 1. Geologic map of the Tremp area (province of Lleida, southern Pyrenees) and location of Maastrichtian hadrosaurid sites (based on Losantos et al. 1989).

The aim of the present contribution is to describe new hadrosaurian material from the province of Lleida and to discuss its phylogenetic significance within the European framework. The biogeographical implications of this find are discussed as well.

Geological setting

Five hadrosaurian localities are currently known in Lleida (Figure 1): Moró, Vilamitjana, Sant Romà d'Abella, Abella de la Conca and Fontllonga. All but Fontllonga are located in the Pallars Jussà region and geologically belong to the Tremp Basin. These localities are Maastrichtian in age (Tremp Formation, Suterranya Sequence, sensu Ardévol et al. 1995).

The Fontllonga site is situated in the Noguera region, on the southern limb of the Ager syncline. The continental red beds of the Tremp Formation (informally known as 'Garumnian') are well exposed in the core of both the Tremp Basin and Ager syncline, which are separated from each other by the Montsec thrust anticline (Figure 1).

The specimen described in the present paper was collected near Fontllonga, between the villages of Camarasa and La Baronia de Sant Oisme. It was found close to the presumed Cretaceous/Tertiary boundary, probably from the last magnetostratigraphic sample of chron 30N (A.S. Schulp, pers. comm.), as interpreted by Galbrun et al. (1993) using palaeomagnetic and biostratigraphic data. This indicates that the fossil was recovered from the uppermost Maastrichtian. The Fontllonga specimen is one of the stratigraphically youngest dinosaur bones from Europe known to date.

Most of the dinosaur bones and eggshells at the Fontllonga section have been recovered from the lower part of Unit 2 of the Tremp Formation (Alvarez Sierra et al. 1994, López Martínez & Vianey-Liaud 1997). On the basis of the stratigraphic position of the presumed uppermost dinosaur remains (found in the chron 31N interval), Galbrun et al. (1993) and Colombo & Cuevas (1993) suggested the disappearance of dinosaurs in the Ager syncline to have occurred about 2 Ma prior to the Cretaceous/Tertiary boundary (see also Colombo 1996, Galbrun 1997). The discovery of new hadrosaurian material in the Fontllonga section invalidates this hypothesis, however, and suggests that dinosaurs survived in this area until the very end of the Cretaceous. This view is also supported by the occurrence of dinosaur footprints located in a precise stratigraphic position only 3 m below the first Palaeocene fossils (chron C29R interval), as pointed out by López Martínez et al. (1998).

Description of new material

The present specimen is a left lower jaw preserving most of the dentary bone and part of the dental battery (Figure 2). The body of the dentary is roughly rectangular, with parallel dorsal and ventral borders. The symphyseal region is broken rostrally to the first alveolar chamber. The coronoid process is very prominent and arises from the lateral surface of the dentary. It extends upwards at a right angle to the longitudinal axis of the dentary to form a large protruding process dorsally. The lateral surface of the coronoid process is strongly convex, while the medial face is slightly concave. The mandibular canal is open along the ventromedial border of the dentary and forms a furrow that becomes wider and deeper caudally. This canal continues caudally as the mandibular fossa, caudal to the base of the coronoid process. The supra-Meckelian canal is oriented obliquely, in contrast to the vertical canal of *Telmatosaurus transsylvanicus* (Le Loeuff et al. 1993). Just caudally of the coronoid process, the dentary ends by two pointed processes above and below the Meckelian groove. The dorsal and medial surfaces of the uppermost dentary process articulate with the splenial, while the caudoventral dentary process articulates with the angular and surangular (see Lambe 1920). The lateral surface of the dentary is

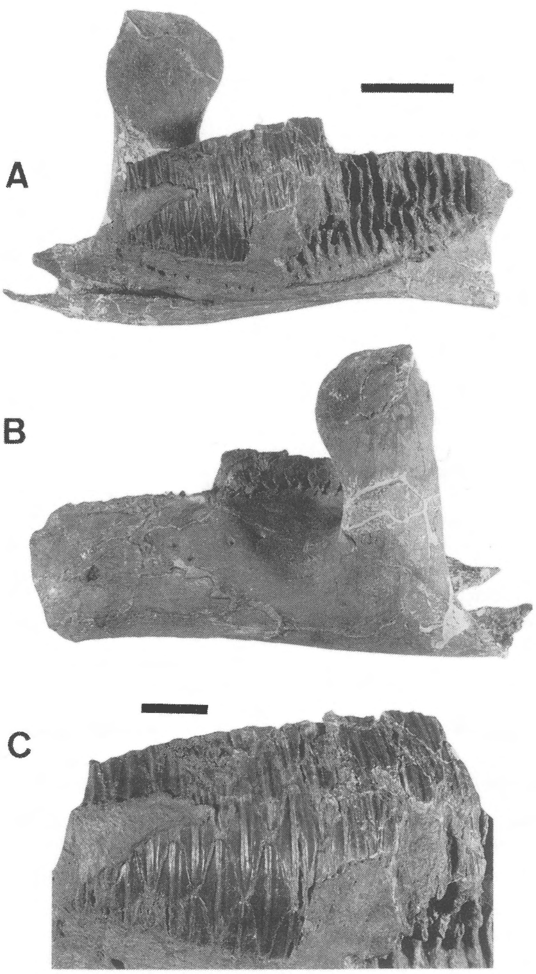

Figure 2. Dentary with teeth from the Maastrichtian of Fontllonga (Ager syncline, province of Lleida). Scale bars represent 5 cm. A: medial view; B: lateral view; C: detail of dentary teeth in lingual view.

convex and perforated by several nutrient foramina for blood vessels and nerves.

The dental battery represents three quarters of the preserved length of the dentary (about 28 cm). It consists of 30 to 31 alveolar chambers; the 14 most rostral alveoli form parallel, vertical furrows, while the most caudal 16 to 17 alveoli show teeth firmly cemented together to form an elaborate battery. The dentary tooth density per 10 cm is 14.5, with a mean alveolar width of about 6.8 mm. Each tooth position consists of four successional teeth, among which two functional teeth and two replacement teeth in the caudal portion of the battery. The mode of tooth replacement in the dental battery does not display a normal hadrosaurian pattern, as identified by Edmund (1960: fig. 47e) and Ostrom (1961: fig. 20). In fact, the distal teeth are not more completely erupted and worn than the central ones and the rows subject to the same replacement are not step-like but more or less horizontal. The significance of this abnormal replacement pattern, as already pointed out by Ostrom (1961), is not well understood. Most of the thin sheet of bone that covers the medial surface of the dental battery is broken, so the dentition is well exposed. A row of special dental foramina (Edmund 1957, 1960) is visible on the ventral border of the battery.

The teeth are characterised by diamond-shaped crowns that are higher than long. The height/mesiodistal length ratio of the dentary crowns is about 2.7. The lingual surface is covered by a thin layer of enamel and bears a prominent median carina; it is linear and slightly displaced distally. A secondary ridge is observed in all preserved teeth, mesially to the median carina. At the basal part of the crown edge, this ridge could be bifid. Some teeth may have a shallow caudal secondary ridge but this condition is not the rule. The crown margins do not display any papillae or denticles, but this may be ascribed to the fact that all preserved teeth are closely interlocked together and that proximal teeth (where denticulations are generally more common) are missing (Coombs 1988; Hall 1993). The angle between the crown and the root seems relatively high, in excess of 130°.

Discussion

Phylogenetic analysis

The character/taxon matrix presented here (Table 1) was compiled from personal observations and, mainly, literature sources (Sereno 1986, Horner 1990, Norman 1990, 1998, Weishampel & Horner 1990, Weishampel et al. 1993, Godefroit et al. 1998). In order to understand the phylogenetic relationships of the Fontllonga hadrosaurid, a cladistic analysis using the HENNIG86 program (Farris 1988) was undertaken. This analysis is based on eight ornithopod taxa and seventeen mandibular and dentary tooth characters. Ingroups include *Iguanodon* species (Norman 1980, 1986), *Ouranosaurus nigeriensis* (see Taquet 1976), *Probactrosaurus gobiensis* (see Rozhdestvenskiy 1967), *Bactrosaurus johnsoni* (see Gilmore 1933; Godefroit et al. 1998), *Telmatosaurus transsylvanicus* (see Nopcsa 1900; Weishampel et al. 1991, 1993), Hadrosaurinae

Table 1. Character taxon data matrix for an outgroup (based on *Hypsilophodon, Camptosaurus* and *Rhabdodon*), eight ingroups, and seventeen mandibular and dentary tooth characters (see text for more details).

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iguanodon	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1
Ouranosaurus	1	1	0	0	0	0	0	1	0	0	0	0	0	1	9	0	0
Probactrosaurus	0	1	1	1	9	0	0	1	0	0	0	0	0	1	9	0	9
Bactrosaurus	0	1	1	1	9	0	0	1	0	0	0	0	0	1	0	1	0
Telmatosaurus	0	2	1	1	1	0	0	1	0	0	0	0	1	1	0	1	0
Hadrosaurinae	1	2	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1
Lambeosaurinae	1	2	1	1	1	1	1	2	1	1	1	1	1	0	0	1	0
Fontllonga	9	2	1	1	1	0	1	1	1	0	0	0	1	0	0	1	0

Derived state characters: 1 = diastema in mandible; 2 = dentary teeth positions: more than 16 (1), more than 29 (2); 3 = three or more dentary teeth per tooth position and more than one replacement dentary tooth; 4 = dental battery formed by crowns firmly cemented together; 5 = dentary alveoli form parallel-sided vertical furrows; 6 = coronoid process inclined rostrally; 7 = miniaturisation of dentary teeth; 8 = high dentary crowns: height/mesiodistal length ratio more than 1.5 (1), more than 3 (2); 9 = dentary teeth not recurved posteriorly; 10 = symmetrical median carina on dentary teeth; 11 = sinuous median carina on dentary teeth; 12 = absence of secondary ridges on dentary teeth; 13 = absence of caudal secondary ridges on dentary teeth; 14 = marginal denticles of dentary crowns supported by subsidiary ridges; 15 = cingulum on dentary teeth; 16 = localisation of enamel to just the lingual surfaces of the dentary crowns; 17 = dentary crown-root angle <130°.

and Lambeosaurinae (see Lull & Wright 1942; Ostrom 1961; Brett-Surman 1989; Horner 1990, 1992; Weishampel & Horner 1990; Weishampel et al. 1993). *Hypsilophodon foxii* (see Galton 1974), *Camptosaurus dispar* (see Gilmore 1909), and *Rhabdodon robustus* (see Nopcsa 1902, 1904) were used as outgroups. Comparisons were also made with other ornithopod taxa, such as *Protohadros byrdi* (see Head, 1998), *Altirhinus kurzanovi* (see Norman 1998), *Dryosaurus lettowvorbecki* (see Sues & Norman 1990), *Tenontosaurus tilletti* (see Ostrom 1970) and *Heterodontosaurus tucki* (see Weishampel & Witmer 1990). *Gilmoreosaurus mongoliensis* (see Gilmore 1933, Brett-Surman 1979) and other problematic taxa were not included in this study because their anatomy is very poorly known. Pending a complete revision of these ornithopods, comparisons were made on the basis of the available literature.

The polarity of each character is discussed below. All but two characters are binary. The multistate characters are ordered into three (2 and 8 in Table 1) as follows: (0): plesiomorphic state; (1), (2): apomorphic states. Character state reversal and equivocal synapomorphies are discussed in the text.

Analysis of characters

Character 1: diastema in mandible – Very short or absent (0); long (1). Primitively in Ornithischia, the dentary begins immediately behind the caudal end for the articulation of the predentary (Weishampel et al. 1993). This condition is retained by *Iguanodon*, *Bactrosaurus*, *Probactrosaurus*, and *Telmatosaurus*, in contrast with that found in *Ouranosaurus*, *Protohadros*, lambeosaurines and hadrosaurines, in which a large diastema is formed between the predentary and the first dentary tooth position. This character is not observable in the Fontllonga mandible.

The phylogenetic significance of a mandibular diastema is unclear, but Weishampel et al. (1993), followed by Godefroit et al. (1998), have suggested that it may be a synapomorphy for Lambeosaurinae and Hadrosaurinae (convergently evolved in *Ouranosaurus*). For Norman (1990, 1998), this feature may be of greater importance as a biomechanical indicator than as a phylogenetically important character.

Character 2: number of dentary tooth positions – Fewer than 16 (0); between 16 and 29 (1); more than 29 (2). The number of dentary tooth positions is low, ranging from 10 to 16 in *Hypsilophodon*, *Dryosaurus*, *Camptosaurus*, and *Rhabdodon*. This condition is regarded as primitive for ornithopods. In iguanodontids (sensu Norman, 1990, 1998) there is an increase in the number of dentary teeth per tooth row over that in lower euornithopods: *Iguanodon* has between 21 and 25 dentary teeth according to the different species and *Ouranosaurus* has 23 (Norman & Weishampel 1990). *Bactrosaurus* and *Probactrosaurus* have a similar number of dentary tooth rows (Rozhdestvenskiy 1967, Godefroit et al. 1998). In *Protohadros* there are 28 tooth file positions (Head, 1998). The number of dentary tooth positions is always greater than 29 in higher iguanodontians: 30 in *Telmatosaurus*, 30 to 31 in the Fontllonga mandible, from 30 to 41 in lambeosaurines and up to about 50 in hadrosaurines such as *Edmontosaurus* and *Anatotitan* (Lull & Wright 1942, Brett-Surman 1989). As the number of tooth positions increases during ontogeny (Weishampel 1984), only adult individuals should be taken into account.

Character 3: number of dentary teeth per tooth position – Two (0); three or more (1). In basal ornithischians, the lower dentition is composed of a single functional tooth and a single replacement in each alveolus at each time (Weishampel 1984, Sereno 1991). This condition is also observed in many ornithopods, among them *Hypsilophodon*, *Camptosaurus*, *Rhabdodon*, *Iguanodon*, and *Ouranosaurus* (Weishampel et al. 1993). *Probactrosaurus* shows a possible rudimentary third replacement tooth (Rozhdestvenskiy 1967), and the iguanodontid *Altirhinus* exhibits three dentary teeth in some caudal alveoli (Norman 1998). In *Bactrosaurus*, *Telmatosaurus*, the Fontllonga taxon, hadrosaurines and lambeosaurines, at least three dentary teeth are found per tooth position (Godefroit et al. 1998). The common condition for Hadrosauridae is the presence of three to five teeth per tooth position and from one to three functional teeth in each row at the same time (Lull & Wright 1942, Ostrom 1961, Norman 1984, Weishampel & Horner 1990).

Character 4: dental battery formed of teeth firmly cemented together – Absent (0); present (1). Ancestrally for Ornithischia, the teeth are more or less widely spaced, and each dentary (or maxillary) tooth contributes little to the support of its neighbours (Edmund 1960). In *Camptosaurus* and iguanodontids, there is little evidence of cementum locking the crowns and roots of teeth into a battery, but the individual teeth are coalescent (Sereno 1986, Norman 1990, 1998). In contrast, *Bactrosaurus*, *Probactrosaurus*, *Telmatosaurus*, the Fontllonga mandible, Hadrosaurinae and Lambeosaurinae have the teeth firmly cemented together to form a compact dental battery, being the interlocking of the individual roots and crows very efficient (Edmund 1960, Ostrom 1961).

Character 5: dentary alveoli form parallel-sided vertical furrows – Absent (0); present (1). In primitive ornithischians and basal ornithopods, each dentary tooth is individually lodged in a discrete socket or alveolus. The teeth of *Camptosaurus*, *Iguanodon* and *Ouranosaurus* tend to lie in a continuous groove, although the teeth are independently affixed to the jaw (Edmund 1960). In *Telmatosaurus*, the Fontllonga mandible and all other hadrosaurids, the dentary alveoli form parallel, vertical furrows (Norman 1998). The state of this character in *Bactrosaurus* and *Probactrosaurus* is not well known but it may be intermediate between the iguanodontid and hadrosaurian condition.

Character 6: orientation of the coronoid process – Caudal or nearly straight (0); rostral (1). The primitive condition in reptiles is a coronoid process that arises dorsocaudally or at a right angle with the long axis of the dentary. This character state is retained by most ornithopods, including *Hypsilophodon*, *Camptosaurus*, *Rhabdodon*, *Iguanodon*, *Ouranosaurus*, *Probactrosaurus*, *Bactrosaurus*, *Protohadros*, *Telmatosaurus*, and the Fontllonga mandible. Among hadrosaurids, only the Lambeosaurinae and Hadrosaurinae have the coronoid process rostrally inclined, i.e., towards the orbit rather than towards the supratemporal fossa (Ostrom 1961).

Character 7: dentary tooth crowns – Wide (0); narrow (1). A dentary dentition composed of relatively broad teeth is primitive in Iguanodontia. *Iguanodon*, *Ouranosaurus*, *Probactrosaurus*, *Bactrosaurus*, *Protohadros*, *Telmatosaurus*, and *Gilmoreosaurus* (Weishampel et al. 1993, Norman 1998) retain this condition. On the contrary, in hadrosaurines, lambeosaurines and the Fontllonga mandible, the dentary teeth are much reduced in size. The miniaturisation of dentary teeth is considered a synapomorphy of Euhadrosauria (Weishampel et al. 1993).

Character 8: height/mesiodistal length ratio of dentary crowns – Less than 1.5 (0); from 1.5 to 3 (1); more than 3 (2). In basal euornithopods, the dentary tooth crowns are relatively stout: the functional crowns of *Hypsilophodon*, *Tenontosaurus*, *Rhabdodon*, *Dryosaurus* and *Camptosaurus* are never more than 50%

higher than mesiodistally long. The height/length ratio of dentary crowns ranges between 1.5 and 2 in iguanodontids such as *Iguanodon*, but averages 2.1–2.3 in *Probactrosaurus* and about 2.5 in *Bactrosaurus* (Rozhdestvenskiy 1967). This ratio is about 2.7 in the Fontllonga mandible and, tentatively, *Telmatosaurus*.

The height of the crowns increases in all lambeosaurines when comparing hadrosaurines and the height/mesiodistal length ratio is usually greater than 3 (Horner 1990: fig. 13.4). The relative height of the dentary crowns relative to mesiodistal length may be useful to recognise lambeosaurine teeth, although the dentary teeth change in shape and form during ontogeny, and their shape also changes from the rostral to caudal part of the lower jaw (Coombs 1988, Brett-Surman 1989).

Character 9: form of dentary teeth – Recurved (0); not recurved (1). The dentary tooth crowns in Ornithopoda are primitively asymmetrical. The dentary crowns are slightly recurved distally in *Hypsilophodon*, *Camptosaurus*, *Rhabdodon*, *Iguanodon*, *Ouranosaurus*, *Bactrosaurus* (Godefroit et al. 1998), and *Probactrosaurus* (Lu, 1997). *Telmatosaurus* and *Protohadros* retain the ancestral condition, unlike all other hadrosaurids (with the possible exception of *Claosaurus* and *Gilmoreosaurus*; see Weishampel et al. 1993), in which the dentary teeth are not recurved. This character, shared by hadrosaurines, lambeosaurines and the Fontllonga mandible, constitutes a synapomorphy for Euhadrosauria.

Character 10: position of the median carina relative to the midline of the dentary crown – Asymmetrical (0); symmetrical (1). The median carina is symmetrically placed relative to the midline of the dentary crown in hadrosaurines and lambeosaurines, and this character appears to be derived for this clade (Jagt et al. 1998). All the lower forms, including the Fontllonga taxon, *Telmatosaurus*, *Protohadros*, *Bactrosaurus*, *Probactrosaurus* and iguanodontids, have an asymmetrically placed median carina, which is slightly displaced distally on dentary crowns.

Character 11: shape of the median carina on dentary teeth – Linear (0); sinuous (1). The median carina of the lambeosaurine dentary crowns is sinuous, in contrast to remaining hadrosaurids, in which the median carina is linear or slightly curved (Weishampel & Horner 1990). The sinuous shape of the median carina is a synapomorphy shared by *Corythosaurus*, *Hypacrosaurus*, *Parasaurolophus* and *Lambeosaurus* (see Horner 1990, Weishampel & Horner 1990). On the contrary, the dentary teeth of *Iguanodon*, *Ouranosaurus*, *Bactrosaurus*, *Probactrosaurus*, *Telmatosaurus* and the Fontllonga mandible retain the primitive condition.

Character 12: secondary ridges on dentary teeth – Present (0); absent (1). Unlike basal ornithopods, the lingual enamelled surface of the dentary teeth of hypsilophodontids, iguanodontids and primitive hadrosauroids is ornamented by a series of mesial and distal longitudinal ridges (Weishampel 1984). This pattern is more complex in iguanodontids than in hypsilophodontids. Secondary ridges are present in *Hypsilophodon*, *Dryosaurus*, *Camptosaurus*, *Rhabdodon*, *Iguanodon*, *Ouranosaurus*, *Altirhinus*, *Probactrosaurus*, *Bactrosaurus*, *Protohadros* and *Telmatosaurus*. A mesial secondary ridge can be observed in all the dentary crowns of the Fontllonga mandible. The dentary teeth of both hadrosaurines and lambeosaurines lack secondary ridges, however, with the possible exception of some teeth of *Parasaurolophus* (see Horner 1990: fig. 13.4d) and a juvenile hadrosaurid from New Mexico (Hall 1993). The absence of secondary ridges on the dentary teeth is here regarded as the derived condition among the Hadrosauridae.

Character 13: distal secondary ridges on dentary crowns – Present (0); absent (1). As mentioned above, the presence of secondary ridges on dentary teeth is a common condition among Euornithopoda. *Telmatosaurus* differs from *Bactrosaurus*, *Probactrosaurus* and iguanodontids in the absence of distal secondary ridges on dentary teeth (Godefroit et al. 1998). The derived condition is also observed in the Fontllonga taxon (although some crowns may have a shallow distal ridge), Hadrosaurinae and Lambeosaurine. Thus, this character constitutes a synapomorphy for Hadrosauridae (see below).

Character 14: marginal denticles of dentary teeth supported by subsidiary ridges – Absent (0); present (1). Primitively in Ornithischia, denticles are present along the margins of dentary teeth, but they are not supported (i.e., are not confluent with) ridges on the lingual surface of crowns (Weishampel & Heinrich 1992). This condition is retained in *Camptosaurus*, *Dryosaurus* and *Tenontosaurus*. On the contrary, marginal denticles are supported by ridges in all hypsilophodontids except *Hypsilophodon* (reversal state; Weishampel & Heinrich 1992).

In *Iguanodon*, *Ouranosaurus*, and *Altirhinus*, the dentary teeth have a variable number of third-order ridges which run down the crown surface taking usually their origin from the bases of the marginal denticles (Norman & Weishampel 1990, Norman 1998). The mesial denticles of dentary crowns are supported by short ridges in *Probactrosaurus*, *Bactrosaurus* and *Telmatosaurus* (Lu, 1997, Godefroit et al. 1998). In contrast, the teeth of the Fontllonga mandible, hadrosaurines and lambeosaurines are devoid of it. The absence of subsidiary ridges supporting the marginal denticles of dentary teeth may be a secondary loss and is here considered as a synapomorphy of Euhadrosauria. This feature arose independently in Hypsilophodontidae (Weishampel & Heinrich 1992).

Character 15: cingulum on dentary crowns – Absent (0), present (1). Among ornithopods, the absence of a basal cingulum on dentary crowns, as observed in *Heterodontosaurus*, *Camptosaurus*, *Tenontosaurus*, *Rhabdodon* and *Dryosaurus*, is the primitive condition (Weishampel & Witmer 1990, Weishampel & Heinrich 1992). A cingulum at the base of the dentary crowns is developed to some degree in all hypsilophodontids; it is interpreted as a derived feature among these taxa (Weishampel & Heinrich 1992). An oblique cingulum is developed just below the widest part of the crown on some iguanodontid teeth, e.g., *Iguanodon* (Norman & Weishampel 1990). The absence of a basal cingulum on the dentary teeth of *Bactrosaurus*, *Telmatosaurus*, the Fontllonga mandible, hadrosaurines and lambeosaurines may be a reversal character and thus diagnose Hadrosauroidea. Another alternative interpretation is that a cingulum on dentary teeth was acquired independently by Hypsilophodontidae and *Iguanodon*.

Character 16: enamel completely localised on the lingual surfaces of the dentary crowns – Absent (0); present (1). Primitively in Ornithopoda, the crown surfaces of the cheek teeth are uniformly enamelled (Weishampel 1984). Enamel is found predominantly on the medial side of the dentary teeth in *Heterodontosaurus*, *Hypsilophodon*, *Iguanodon* and related ornithopods, but is retained as a thin veneer on the lateral surface of the dentary crowns (Norman 1990, Norman & Weishampel 1990, Sues & Norman 1990). In *Telmatosaurus*, the Fontllonga specimen, hadrosaurines and lambeosaurines, the enamel is absent from the lateral side of the dentary crowns and completely localised on the lingual surface (Norman 1990). This condition appears to be absent in *Probactrosaurus* (Norman 1998) but may be developed in *Bactrosaurus* (Godefroit et al. 1998). The restricted distribution of enamel on the occlusal surfaces of the hadrosaurian teeth probably contributed to a rapid tooth wear and a highly effective replacement mechanism (Ostrom 1961).

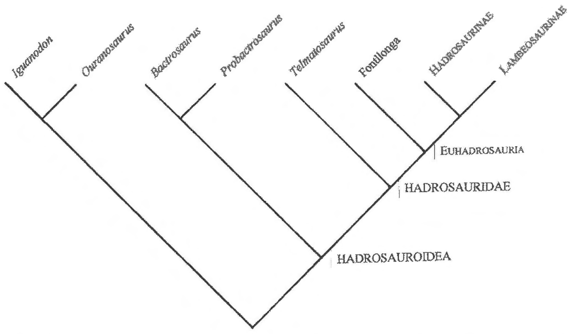

Figure 3. Cladogram showing the phylogenetic relationships of the Fontllonga hadrosaurid (see Table 1).

Character 17: angle between the crown and root of dentary teeth – Over 130° (0); less than 130° (1). Among ankylopollexian iguanodontians (sensu Sereno 1986; Camptosauria of Norman 1998), the angle between the crown and root is primitively relatively high (i.e. > 130°) in *Camptosaurus*, *Ouranosaurus*, *Telmatosaurus*, *Bactrosaurus*, the Fontllonga taxon and Lambeosaurinae (Weishampel et al. 1993, Godefroit et al. 1998). In typical Hadrosaurinae, *Claosaurus*, *Protohadros* and species of *Iguanodon*, the angle is less than 130° (Sternberg 1936, Langston 1960, Horner 1990, Head 1998). Horner (1990) interpreted this feature as a derived character of *Iguanodon* plus hadrosaurines, a clade which he called Hadrosauria. Here we follow Weishampel et al. (1993) in regarding this character as a synapomorphy for Hadrosaurinae, convergently evolved in *Iguanodon*.

Results

The analysis of the character-taxon matrix presented in Table 1 generated a single most parsimonious tree, with a consistency index of 0.79 and a retention index of 0.69 (Figure 3).

On the basis of this analysis, the Fontllonga taxon is considered to be more derived than *Telmatosaurus transsylvanicus* and to represent a member of the Euhadrosauria clade (sensu Weishampel et al. 1993). Euhadrosaurians share the following synapomorphies: (1) miniaturisation of dentary teeth [character 7], (2) dentary teeth not recurved [character 9], and (3) marginal denticles of dentary crowns not supported by subsidiary ridges (secondary loss) [character 14].

The Fontllonga taxon lacks a number of derived features that characterise both Hadrosaurinae and Lambeosaurinae. This clade is diagnosed as follows: (1) coronoid process inclined rostrally [character 6], (2) symmetrical median carina on dentary teeth [character 10], and (3) absence of secondary ridges on dentary teeth [character 12].

The present study does not support the diphyletic origin of the hadrosaurids, but regards this group as monophyletic (see Weishampel & Horner 1990, Norman 1990, Weishampel et al. 1993, Forster 1997). The monophyly of Hadrosauridae is supported by the following synapomorphies: (1) more than 29 dentary teeth positions [character 2.2], (2) dentary alveoli form parallel-sided vertical furrows [character 5], (3) absence of distal secondary ridges on dentary teeth [character 13], and (4) localisation of enamel to just the lingual surfaces of the dentary crowns [character 16].

Other hadrosaurid synapomorphies are listed by Weishampel & Horner (1990) and Weishampel et al. (1993). It should be noted that Forster (1997) proposed a new definition for Hadrosauridae, restricting this clade to Lambeosaurinae plus Hadrosaurinae (see also Godefroit et al. 1998). This interpretation is not consistent, however, with the original definition of Hadrosauridae. This name was erected by Cope (1869), based on a diagnosis of tooth remains and including a host of fairly poorly known forms (species of *Hadrosaurus*, *Trachodon*, *Diclonius*, *Hypsibema*, *Ornithotharsus*, *Claosaurus*, *Cionodon* and *Orthomerus*). Most of these taxa are now considered nomina dubia (Weishampel & Horner 1990).

Telmatosaurus (originally named *Limnosaurus* by Nopcsa 1900) constitutes the first of these early named forms to contribute to Cope's taxon Hadrosauridae legitimately, by quality and longevity. On the other hand, the subfamilies Hadrosaurinae and Lambeosaurinae were not recognised until 1923 (Lambe 1918, Parks 1923). Following Nopcsa's work, *Telmatosaurus* must be considered a member of the Hadrosauridae. The analyses in the present contribution indicate (cf. Weishampel et al. 1993) that *Telmatosaurus* is neither euhadrosaurian (as suggested by Norman 1998) nor a derived iguanodontian (Forster 1997), but a basal hadrosaurid.

Within the Hadrosauridae, lambeosaurines share high dentary crowns bearing a sinuous median carina [characters 8 and 11]. Hadrosaurines are characterised by a dentary crown-root angle less than 130° [character 17]. The cladogram of Figure 3 supports the basal position of *Bactrosaurus johnsoni* among the Hadrosauroidea (see Godefroit et al. 1998). Hadrosauroids can be diagnosed on the following synapomorphies: (1) three or more dentary teeth per tooth position, including more than one replacement tooth [character 3], (2) dental battery formed by crowns firmly cemented together [character 4], and (3) absence of a cingulum on dentary teeth (secondary loss) [character 15].

Sereno (1986) erected the superfamily Hadrosauroidea for the reception of the Hadrosauridae and *Ouranosaurus*. Following the recent works by Norman (1990) and Godefroit et al. (1998), *Ouranosaurus* is excluded from the Hadrosauroidea because it lacks a set of synapomorphies. The position of *Probactrosaurus* is uncertain. Sereno (1986) considered this as a taxon more distantly related to hadrosaurids than to either *Iguanodon* or *Ouranosaurus*, whereas Norman (1990) regarded it as a sister-taxon of the Hadrosauridae. The present study suggests that *Probactrosaurus* shares at least two hadrosauroid synapomorphies [characters 3 and 4]. Pending a full revision of this taxon, *Probactrosaurus* is here tentatively regarded as a basal hadrosauroid. *Protohadros byrdi* could be either a derived iguanodont (sensu Norman & Weishampel 1990) or the most basal hadrosaurid (Head 1998). It exhibits some hadrosaurid synapomorphies [characters 5 and 13] but lacks at least one [character 2.2]. If *Protohadros* is considered the most basal member of Hadrosauridae, the clade should be redefined (Head 1998). Finally, the status of the family Iguanodontidae (supported as valid by Norman 1990, 1998) is not discussed here. According to Norman (1998), the Iguanodontidae includes *Iguanodon*, *Ouranosaurus*, *Altirhinus* and *Lurdusaurus* (Taquet & Russell 1999).

Implications

The Fontllonga specimen provides new data on the diversity of European hadrosaurids at the end of the Cretaceous. Until now, two species were recognised in the Maastrichtian of Europe, viz. the basal hadrosaurid *Telmatosaurus transsylvanicus* from the Haţeg Basin (Romania; see Nopcsa 1900, Weishampel et al. 1991,

1993) and the lambeosaurine *Pararhabdodon isonensis* from the Tremp Basin (Catalonia; see Casanovas et al. 1993, 1997, 1999). *Orthomerus dolloi* from Liège-Limburg is based on non-diagnostic material (Seeley, 1883, Brinkmann 1988) and is generally considered a nomen dubium. *Telmatosaurus* has also been described beyond Transylvania (Mulder 1984, Le Loeuff et al. 1993), but this should be taken with caution. With regard to *Pararhabodon*, it is probably represented by fragmentary material in Languedoc (Laurent et al. 1997). All remaining hadrosaurid material of Europe is provisionally interpreted as Hadrosauridae indet. (Brinkmann 1988). Recently, the occurrence of euhadrosaurian remains in Liège-Limburg has been suggested (Jagt et al. 1998, Weishampel et al. 1999). Euhadrosaurian hadrosaurids may also be represented in the uppermost Cretaceous of Valencia (Company et al. 1998).

The Fontllonga dentary differs from that of *Telmatosaurus transsylvanicus* in a number of tooth characters (see above). An accurate comparison with *Pararhabdodon isonensis* is difficult because the mandible of the latter preserves no tooth in place. Nevertheless, a preliminary cladistic analyis of *Pararhabdodon* suggests that it is a basal member of the Lambeosaurinae (Casanovas et al. 1999), and represents a more derived taxon than the Fontllonga hadrosaurid. Our study indicates that the Fontllonga taxon is a primitive euhadrosaurian but the material is inadequate for the erection of a new species. On the basis of the knowledge currently available, it is referred to as Euhadrosauridae indet.

The basal position of the Fontllonga taxon among Euhadrosauria is at first glance paradoxical with its late Maastrichtian age. To explain the evolutionary traits and temporal distribution of the Fontllonga species requires an understanding of the palaeobiogeographical history of the Hadrosauridae. The earliest appearance of hadrosaurids (and probably euhadrosaurians) extends to the mid-Cretaceous of western North America (Kirkland et al. 1997, Head 1998) and Asia (Norman 1998), and the oldest European record is late Albian (Lydekker 1888). Thus, the sister-group relationship between the Fontllonga euhadrosaurian and the clade Hadrosaurinae plus Lambeosaurinae indicates a high 'minimum divergence time' (or 'ghost lineage duration'; see Weishampel 1996). This relationship implies a minimum divergence time of at least 25 million years between the earliest appearance of Euhadrosauria and the occurrence of the Fontllonga species. It is suggested that populations of euhadrosaurian hadrosaurids were able to disperse from Asia to Europe during the latest Early Cretaceous (see Russell 1993, Norman 1998) and, after the development of geographical barriers, were able to survive in isolation in the European archipelago. The occurrence of basal hadrosaurids such as *Telmatosaurus* in the latest Cretaceous of Europe could be explained in terms of geographical isolation as well (Weishampel et al. 1993).

Conclusions

The discovery of new hadrosaurian material in the uppermost Cretaceous of Fontllonga is worthy of consideration for several reasons. At first, it indicates the occurrence of a third species of hadrosaurid different from *Telmatosaurus transsylvanicus* and *Pararhabdodon isonensis* in the Maastrichtian of southern Europe. Moreover, it provides useful information about the evolutionary stages of dental batteries within hadrosaurids. The Fontllonga hadrosaurid is more derived than *Telmatosaurus* in having narrow dentary teeth not recurved distally. Nevertheless, it lacks a number of derived features that characterise the clade Hadrosaurinae plus Lambeosaurinae, e.g., coronoid process inclined rostrally, symmetrical median carina, and lack of secondary ridges on dentary crowns. Based on these characteristics, the Fontllonga taxon is here regarded as a basal member of the Euhadrosauria.

The present find is interesting for palaeobiogeographical reasons. The late appearance of a basal euhadrosaurian in the Iberian peninsula evidences the survival of primitive hadrosaurids in the European archipelago during the latest Cretaceous. This supports the idea that European hadrosaurids were evolutionary relict taxa, isolated from North American and Asian relatives during the Late Cretaceous.

Acknowledgements

The specimen was discovered and collected by Remmert Schouten and Anne S. Schulp (Natuurhistorisch Museum Maastricht) when prospecting in the Ager syncline; we thank the latter for kindly providing information on its stratigraphic position. The preparation was done by Valérie Delforno and Remmert Schouten at the Musée des Dinosaures (Espéraza, France). We are grateful to Sandra Chapman (Natural History Museum, London) for access to specimens in her care and to Julio Company (Universitat de València) for discussions on hadrosaurian topics. We also thank an anonymous referee for suggesting improvements to the manuscript.

References

Alvarez Sierra, M.A., M.E. Arribas, L. Ardévol, J. Civis, R. Daams, S. Krauss, N. López Martínez, A. de la Peña, R. Soler, M. Vianey-Liaud, A. Lacasa, B. Marandat, P. Peláez Campomanes, P. Sevilla & B. Sigé 1994 El límite Cretácico-Terciario en la sección de la Fontllonga (Cuenca de Ager, provincia de Lérida) – Com. II Congr. G.E.T. (Jaca): 23–26

Ardévol, L., M.L. Casanovas & J.V. Santafé 1995 Restos de dinosaurios del Maastrichtiense de la Conca de Tremp, Lleida (cuenca de antepais Pirenaica Meridional). In: López, G., A. Obrador & E. Vicens (eds) XI Jorn. Paleont. Tremp: 25–27

Brett-Surman, M.K. 1979 Phylogeny and palaeobiogeography of hadrosaurian dinosaurs – Nature 277: 560–562

Brett-Surman, M.K. 1989 A Revision of the Hadrosauridae and their Evolution during the Campanian and Maastrichtian – PhD Thesis George Washington Univ., Washington, D.C.

Brinkmann, W. 1984 Erster Nachweis eines Hadrosauriers (Ornithischia) aus dem unteren Garumnium (Maastrichtium) des Beckens von Tremp (Provinz Lérida, Spanien) – Paläont. Z. 58: 295–305

Brinkmann, W. 1988 Zur Fundgeschichte und Systematik der Ornithopoden (Ornithischia, Reptilia) aus der Ober-Kreide von Europa – Docum. Nat. 45: 1–157

Casanovas, M.L. 1992 Novedades en el registro fósil de dinosaurios del Levante español – Zubia 10: 139–151

Casanovas, M.L., X. Pereda Suberbiola & J.V. Santafé 1998 Hadrosaurid dinosaurs from the Pre-Pyrenees of Catalonia. In: Jagt, J.W.M., P.H. Lambers, E.W.A. Mulder & A.S. Schulp (eds) 3rd Eur. Workshop Vert. Palaeont., Maastricht, Abstr.: 16–17

Casanovas, M.L., X. Pereda Suberbiola, J.V. Santafé & D.B. Weishampel 1999 First lambeosaurine hadrosaurid from Europe: palaeobiogeographical implications – Geol. Mag. 136 (2): 205–211

Casanovas, M.L., J.V. Santafé, J.L. Sanz & A.D. Buscalioni 1985 *Orthomerus* (Hadrosaurinae, Ornithopoda) del Cretácico superior del yacimiento de 'Els Nerets' (Tremp, España) – Paleont. Evol. 19: 155–162

Casanovas, M.L., J.V. Santafé, J.L. Sanz & A.D. Buscalioni 1986 *Orthomerus* (Hadrosaurinae, Ornithopoda) du Crétacé supérieur du gisement de 'Els Nerets' (Tremp, Lleida). In: Les dinosaures de la Chine à la France – Mus. Hist. Nat. Toulouse: 99–111

Casanovas, M.L., J.V. Santafé, J.L. Sanz & A.D. Buscalioni 1987 Arcosaurios (Crocodilia, Dinosauria) del Cretácico superior de la Conca de Tremp (Lleida, España) – Estud. Geol., vol. extr. Galve-Tremp: 95–110

Casanovas, M.L., J.V. Santafé & A. Isidro 1993 *Pararhabdodon isonense* n. gen. n. sp. (Dinosauria). Estudio morfológico, radio-tomográfico y consideraciones biomecánicas – Paleont. Evol. 26–27: 121–131

Casanovas, M.L., J.V. Santafé, J.L. Sanz & J.E. Powell 1995 Nuevos restos de dinosaurios (Titanosauria y Ornithopoda) en el Cretácico superior de las Cuencas de Tremp y Dellà (Lleida, España) – Estud. Geol. 51: 277–283

Casanovas, M.L., J.V. Santafé & X. Pereda Suberbiola 1997 Nouveaux restes de *Pararhabdodon isonensis* (Dinosauria, Hadrosauridae) et synthèse de l'ensemble du matériel découvert dans le Crétacé supérieur de Catalogne. In: 2nd Eur. Workshop Vert. Palaeont., Espéraza-Quillan, Abstr.

Colombo, F. 1996 Stratigraphic and sedimentary characteristics of the Cretaceous-Tertiary boundary in the Ager basin, Lleida Province, Spain. In: McLeod, N. & G. Keller (eds) Cretaceous-Tertiary Mass Extinctions. Biotic and Environmental Changes. W.W. Norton and Co., New York: 399–413

Colombo, F. & Cuevas, J.L. 1993 Características estratigráficas y sedimentológicas del 'Garumniense' en el sector de Ager (Pre-Pirineo, Lleida) – Acta Geol. Hisp. 28: 15–23

Company, J., A. Galobart & R. Gaete 1998 First data on the hadrosaurid dinosaurs from the Upper Cretaceous of Valencia, Spain – Oryctos 1: 121–126

Coombs Jr., W.P. 1988 The status of the dinosaurian genus *Diclonius* and the taxonomic utility of hadrosaurian teeth – J. Paleont. 62: 812–817

Cope, E.D. 1869 Synopsis of the extinct Batrachia, Reptilia, and Aves of North America – Trans. Amer. Phil. Soc. 15: 1–252

Edmund, A.G. 1957 On the special foramina in the jaws of many ornithischian dinosaurs – Palaeont. Contr. R. Ontario Mus. Zool. 48: 1–14

Edmund, A.G. 1960 Tooth replacement phenomena in the Lower Vertebrates – R. Ontario Mus., Life Sci. Div. 52: 1–190

Farris, J.S. 1988 HENNIG86 version 1.5 Copyright – Farris

Forster, C.A. 1997 Phylogeny of the Iguanodontia and Hadrosauridae – J. Vert. Paleont. 17 (Suppl. to 3): 47A

Galbrun, B. 1997 Did the European dinosaurs disappear before the K-T event? Magnetostratigraphic evidence – Earth Planet. Sci. Lett. 148: 569–579

Galbrun, B., M. Feist, F. Colombo, R. Rocchia & Y. Tambareau 1993 Magnetostratigraphy and biostratigraphy of Cretaceous-Tertiary continental deposits, Ager Basin, Province of Lerida, Spain – Palaeogeogr., Palaeoclimatol., Palaeoecol. 102: 41–52

Galton, P.M. 1974 The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight – Bull. Brit. Mus. (Nat. Hist.), Geol. 25: 1–152

Gilmore, C.W. 1909 Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and descriptions of two new species – Proc. U.S. Nat. Mus. 36: 197–332

Gilmore, C.W. 1933 On the dinosaurian fauna of the Iren Dabasu Formation – Bull. Amer. Mus. Nat. Hist. 67: 23–78

Godefroit, P., Z.M. Dong, P. Bultynck, H. Li & L. Feng 1998 Sino-Belgian Cooperation Program 'Cretaceous Dinosaurs and Mammals from Inner Mongolia'. 1. New *Bactrosaurus* (Dinosauria: Hadrosauroidea) material from Iren Dabasu (Inner Mongolia, P.R. China) – Bull. Inst. R. Sci. Nat. Belg., Sci. Terre 68 (Suppl.): 3–70

Hall, J.P. 1993 A juvenile hadrosaurid from New Mexico – J. Vert. Paleont. 13: 367–369

Head, J.J. 1998 A new species of basal hadrosaurid (Dinosauria, Ornithischia) from the Cenomanian of Texax – J. Vert. Paleont. 18: 718–738

Horner, J.H. 1990 Evidence of diphyletic origination of hadrosaurian (Reptilia: Ornithischia) dinosaurs. In: Carpenter, K. & P.J. Currie (eds) Dinosaur Systematics: Perspectives and Approaches. Cambridge Univ. Press, Cambridge: 179–187

Horner, J.H. 1992 Cranial morphology of *Prosaurolophus* (Ornithischia; Hadrosauridae) with descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relations – Mus. Rockies Occ. Papers 2: 1–119

Jagt, J.W.M., R.W. Dortangs, M.M.M. Kuypers, E.W.A. Mulder, A.S. Schulp & D.B. Weishampel 1998 Dinosaur remains in the type Maastrichtian: an update. In: Jagt, J.W.M., P.H. Lambers, E.W.A. Mulder & A.S. Schulp (eds) 3rd Eur. Workshop Vert. Palaeont., Maastricht, Abstr.: 35

Kirkland, J.I., B. Britt, D.L. Burge, K. Carpenter, R. Cifelli, F. Decourten, J. Eaton, S. Hasiotis & T. Lawton 1997 Lower to Middle Cretaceous dinosaur faunas of the Central Colorado Plateau: key to understanding 35 My of tectonics, sedimentology, evolution and biogeography – Brigham Young Univ. Geol. Stud. 42: 69–103

Lambe, L.M. 1918 On the genus *Trachodon* of Leidy – Ottawa Nat. 31: 135–139

Lambe, L.M. 1920 The hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta – Geol. Surv. Mem., Can. Dept Min., Geol. Ser. 120: 1–79

Langston, W., J.R. 1960 The vertebrate fauna of the Selma Formation of Alabama. Part VI. The dinosaurs – Fieldiana (Geol.) 3: 315–361

Laurent, Y., J. Le Loeuff & E. Buffetaut 1997 Les Hadrosauridae (Dinosauria, Ornithopoda) du Maastrichtien supérieur des Corbières orientales (Aude, France) – Rev. Paléobiol. 16: 411–423

Le Loeuff, J., E. Buffetaut, M. Martin, V. Martin & H. Tong 1993 Découverte d'Hadrosauridae (Dinosauria, Ornithischia) dans le Maastrichtien des Corbières (Aude, France) – C.R. Acad. Sci. Paris 316(2): 1023–1029

López Martínez, N. & M. Vianey-Liaud 1997 Late Cretaceous dinosaur eggshells from the Tremp Basin, southern Pyrenees, Lleida, Spain – J. Paleont. 71: 1157–1171

López Martínez, N., L. Ardévol, M.E. Arribas, J. Civis & A. González Delgado 1998 The geological record in non-marine environments around the K/T boundary (Tremp Formation, Spain) – Bull. Soc. Géol. France 169: 11–20

Losantos, M., E. Aragonés, X. Berastegui, J. Palau & C. Puigdefabregas 1989 Mapa geològic de Catalunya 1:250.000 – Serv. Geol. General. Catalunya, Barcelona

Lu, J. 1997 A new Iguanodontidae (*Probactrosaurus mazongshanensis* sp. nov.) from Mazongshan area Gansu Province, China. In: Dong, Z. (ed.) Sino-Japanese Silk Road Dinosaur Expedition. China Ocean Press, Beijing: 27–47

Lull, R.S. & N.E. Wright 1942 Hadrosaurians dinosaurs of North America – Geol. Soc. Amer., Spec. Pap. 40: 1–242

Lydekker, R. 1888 Note on a new Wealden iguanodont and other dinosaurs – Q. J. Geol. Soc. London 44: 46–61

Mulder, E.W.A. 1984 Resten van *Telmatosaurus* (Ornithischia, Hadrosauridae) uit het Boven-Krijt van Zuid-Limburg – Grondb. Hamer 38: 108–115

Mulder, E.W.A., M.M.M. Kuypers, J.W.M. Jagt & H.H.G. Peeters 1997 A new late Maastrichtian hadrosaurid dinosaur record from northeast Belgium – N. Jb. Geol. Paläont. Mh. 1997/6: 339–347

Nopcsa, F. 1900 Dinosaurierreste aus Siebenbürgen. I. Schädel von *Limnosaurus transsylvanicus* nov. gen. et spec. – Denkschr. K. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 68: 555–591

Nopcsa, F. 1902 Dinosaurierreste aus Siebenbürgen II (Schädelreste von *Mochlodon*) – Denkschr. Akad. Wiss., Math.-Naturwiss. Kl. 72: 149–175

Nopcsa, F. 1904 Dinosaurierreste aus Siebenbürgen III (Weitere Schädelreste von *Mochlodon*) – Denkschr. Akad. Wiss., Math.-Naturwiss. Kl. 74: 229–263

Norman, D.B. 1980 On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium) – Mém. Inst. R. Sci. Nat. Belg. 178: 1–103

Norman, D.B. 1984 On the cranial morphology and evolution of ornithopod dinosaurs – Symp. Zool. Soc. London 52: 521–547

Norman, D.B. 1986 On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda) – Bull. Inst. R. Sci. Nat. Belg., Sci. Terre 56: 281–372

Norman, D.B. 1990 A review of *Vectisaurus valdensis*, with comments on the family Iguanodontidae. In: Carpenter, K. & P.J. Currie (eds) Dinosaur Systematics: Perspectives and Approaches. Cambridge Univ. Press, Cambridge: 147–161

Norman, D.B. 1998 On Asian ornithopods (Dinosauria: Ornithischia). 3. A new species of iguanodontid dinosaur. In: Norman, D.B., A.R. Milner & A.C. Milner (eds) A Study of Fossil Vertebrates – Zool. J. Linn. Soc. London 122: 291–348

Norman, D.B. & D.B. Weishampel 1990 Iguanodontidae and related ornithopods. In: Weishampel, D.B., P. Dodson & H. Osmólska (eds) The Dinosauria. Univ. California Press, Berkeley: 510–533

Ostrom, J.H. 1961 Cranial morphology of the hadrosaurian dinosaurs of North America – Bull. Amer. Mus. Nat. Hist. 122: 33–186

Ostrom, J.H. 1970 Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana – Peabody Mus. Nat. Hist. Yale Univ. Bull. 35: 1–234

Parks, W.A. 1923 *Corythosaurus intermedius*, a new species of trachodont dinosaur – Univ. Toronto Stud., Geol. Ser. 15: 1–57

Rozhdestvenskiy, A.K. 1967 New iguanodonts from Central Asia – Int. Geol. Rev. 9: 556–566

Russell, D.A. 1993 The role of Central Asia in dinosaurian biogeography – Can. J. Earth Sci. 30: 2002–2019

Santafé, J.V. & M.L. Casanovas 1993 Dinosaurios en la Comunidad Valenciana – General. Valenciana, Valencia

Seeley, H.G. 1883 On the dinosaurs from the Maastricht Beds – Q. J. Geol. Soc. London 39: 246–253

Sereno, P.C. 1986 Phylogeny of the bird-hipped dinosaurs (Order Ornithischia) – Nat. Geogr. Soc. Res. 2: 234–256

Sereno, P.C. 1991 *Lesothosaurus*, 'fabrosaurids', and the early evolution of Ornithischia – J. Vert. Paleont. 11: 168–197

Sternberg, C.M. 1936 The systematic position of *Trachodon* – J. Paleont. 10: 652–655

Sues, H.-D. & Norman, D.B. 1990 Hypsilophodontidae, *Tenontosaurus*, Dryosauridae. In: Weishampel, D.B., P. Dodson & H. Osmólska (eds) The Dinosauria. Univ. California Press, Berkeley: 498–509

Taquet, P. 1976 Géologie et Paléontologie du gisement de Gadoufaoua (Aptien du Niger) – Cah. Paléont. CNRS, Paris: 1–191

Taquet, P & D.A. Russell 1999 A massively-constructed iguanodont from Gadoufaoua, Lower Cretaceous of Niger – Ann. Paléont. 85 (1): 85–96

Weishampel, D.B. 1984 Evolution of jaw mechanisms in ornithopod dinosaurs. In: Advances in Anatomy, Embryology and Cell Biology 87: 1–110

Weishampel, D.B. 1990 Dinosaurian distribution. In: Weishampel, D.B., P. Dodson & H. Osmólska (eds) The Dinosauria. Univ. California Press, Berkeley: 63–140

Weishampel, D.B. 1996 Fossils, phylogeny, and discovery: a cladistic study of the history of tree topologies and ghost lineage durations – J. Vert. Paleont. 16: 191–197

Weishampel, D.B. & R.E. Heinrich 1992 Systematics of Hypsilophodontidae and basal Iguanodontia (Dinosauria: Ornithopoda) – Hist. Biol. 6: 159–184

Weishampel, D.B. & J.H. Horner 1990 Hadrosauridae. In: Weishampel, D.B. P. Dodson & H. Osmólska (eds) The Dinosauria. Univ. California Press, Berkeley: 534–561

Weishampel, D.B. & L.M. Witmer 1990 Heterodontosauridae. In: Weishampel, D.B., P. Dodson & H. Osmólska (eds) The Dinosauria. Univ. California Press, Berkeley: 484–497

Weishampel, D.B., D. Grigorescu & D.B. Norman 1991 The dinosaurs of Transylvania – Nat. Geogr. Res. Expl. 7: 196–215

Weishampel, D.B., D.B. Norman & D. Grigorescu 1993 *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur – Palaeontology 36: 361–385

Weishampel, D.B., E.W.A. Mulder, R.W. Dortangs, J.W.M. Jagt, C.-M. Jianu, M.M.M. Kuypers, H.H.G. Peeters & A.S. Schulp 1999 Dinosaur remains from the type Maastrichtian: an update – Geol. Mijnbouw 78 (3/4): 357–365 (this issue)

Wellnhofer, P. 1994 Ein Dinosaurier (Hadrosauridae) aus der Oberkreide (Maastricht, Helvetikum-Zone) des bayerischen Alpenvorlandes – Mitt. Bayer. Staatsslg Paläont. Hist. Geol. 34: 221–238