

A re-appraisal of *Craspedodon lonzeensis* DOLLO, 1883 from the Upper Cretaceous of Belgium: the first record of a neoceratopsian dinosaur in Europe?

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GODEFROIT P. & LAMBERT O., 2007 – A re-appraisal of *Craspedodon lonzeensis* DOLLO, 1883 from the Upper Cretaceous of Belgium: the first record of a neoceratopsian dinosaur in Europe? *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 77: 83-93, 6 figs, Brussels, October 15, 2007 – ISSN 0374-6291.

Abstract

Craspedodon lonzeensis DOLLO, 1883 is based on three teeth discovered in the Lonzée Member (?Coniacian-Santonian, Upper Cretaceous) in the surroundings of the village of Lonzée (Namur Province, Belgium). Previous authors identified *Craspedodon* as an iguanodontian dinosaur. We rather propose that these fossils belong to a neoceratopsian dinosaur, because of the following characters: the enamelled side of the crown bears deep indentations and a prominent basal cingulum, the opposite side of the crown is very convex vertically and bulbous in mesial view, and secondary ridges start from the apical edge but end prior to the base of the crown. Within Neoceratopsia, it is suggested that *Craspedodon* has more affinities with Ceratopsoidea (*sensu* YOU & DODSON, 2003) than with Protoceratopsidae. It is the first time that ceratopsian dinosaurs are described in Europe. Neoceratopsians probably migrated from Asia into Europe during the Aptian-Albian, when intermittent land bridges were established across the Turgai Straits. This implies a relatively long ghost lineage for neoceratopsians in Europe, of more than nine million years, between their migration towards Europe and their proposed presence in the Lonzée Member.

Keywords: *Craspedodon*, Neoceratopsia, Late Cretaceous, Europe, palaeobiogeography.

Résumé

Craspedodon lonzeensis DOLLO, 1883 est une espèce basée sur trois dents découvertes dans le Membre de Lonzée (?Coniacien-Santonien, Crétacé supérieur), à proximité du village de Lonzée (Province de Namur, Belgique). Des études préalables ont identifié *Craspedodon* comme un Iguanodontia. Mais les caractères suivants rappellent plutôt les Neoceratopsia: la face émaillée de la couronne porte des indentations profondes et un cingulum basal proéminent, la surface opposée de la couronne est verticalement très convexe et bulbeuse en vue médiale, et les crêtes secondaires débutent sur le bord apical mais s'interrompent avant la base de la couronne. Parmi

les Neoceratopsia, nous suggérons que *Craspedodon* possède plus d'affinités avec les Ceratopsoidea (*sensu* YOU & DODSON, 2003, 2004) qu'avec les Protoceratopsidae. C'est la première fois qu'un dinosaure cératopsien est décrit en Europe. Les néocératopsiens ont probablement migré d'Asie en Europe au cours de l'Aptien-Albien, lorsque des ponts terrestres intermittents étaient établis à travers le détroit de Turgai. Cela implique une lignée fantôme relativement longue pour les néocératopsiens en Europe, de plus de neuf millions d'années, entre leur migration vers l'Europe et leur présence proposée au sein du Membre de Lonzée.

Mots-clés: *Craspedodon*, Neoceratopsia, Crétacé supérieur, Europe, paléo-biogéographie.

1. Introduction

The Lonzée Member ('Glauconie de Lonzée') is a highly fossiliferous glauconitic silty clay to sand, only known from the surroundings of the village of Lonzée (Namur Province, Belgium; Fig. 1). The 'glauconie' was

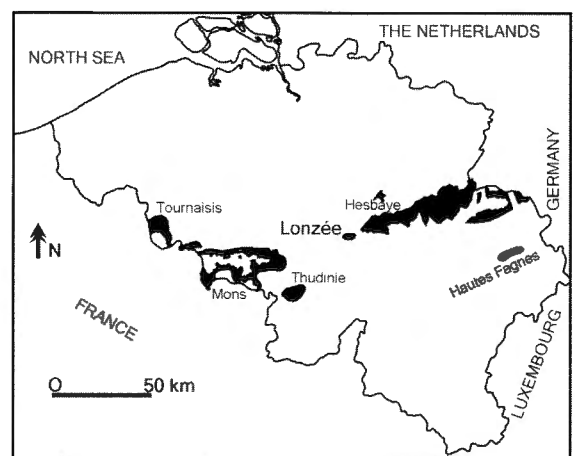


Fig. 1 — Map indicating the geographical location of Lonzée and the distribution of Cretaceous outcrops (in black) in Belgium (modified from MALCHUS *et al.*, 1994).

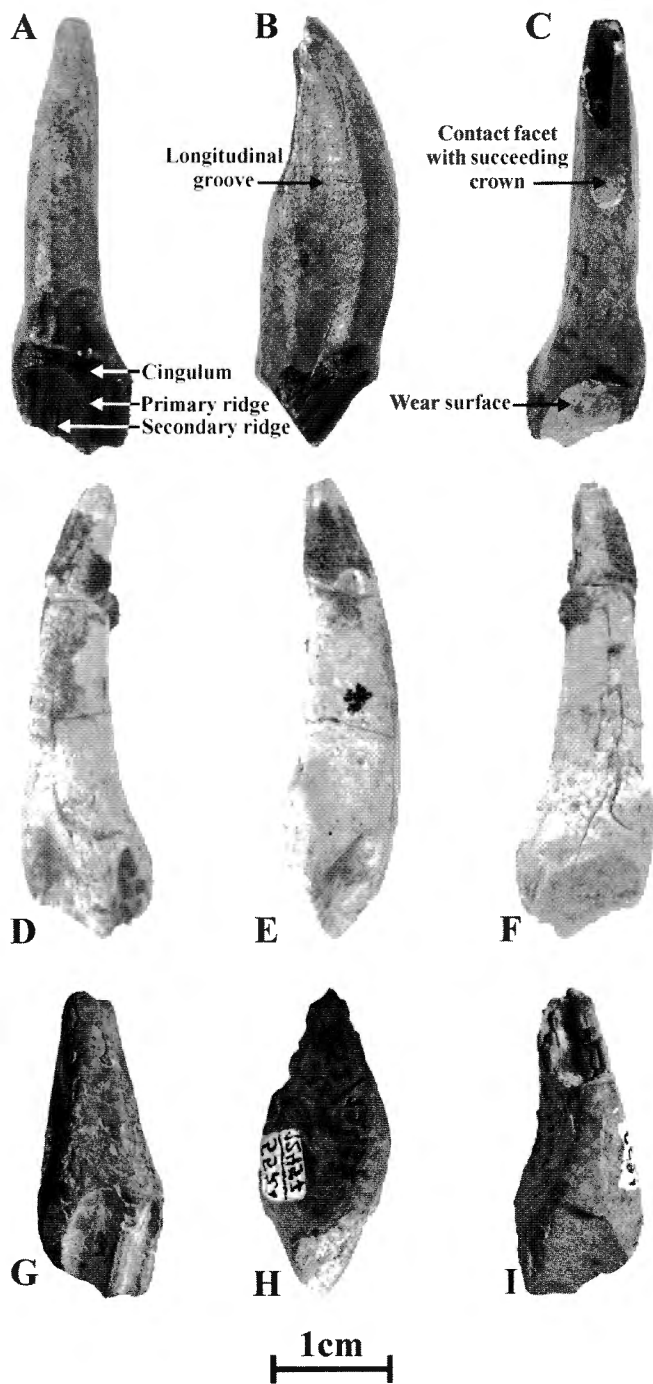


Fig. 2 — Comparison of a ?left maxillary tooth of *Craspedodon lonzeensis* (A-C: IRSNB R59), from the Upper Cretaceous of Lonzeée, with that of the neoceratopsian *Protoceratops hellenikorhinus* (D-F: IMM 96BM5/2), from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China) and that of the neoceratopsian *Turanoceratops tardabilis* (G-I: TsNIGRI 552/12457: mirror images), from the Upper Cretaceous of Dzharakhukuk (Uzbekistan). A, D and G: labial views; B and E: ?mesial views; H: ?distal view; C, F and I: lingual views.

exploited until 1914 because of its colouring properties. The belemnites at Lonzeée indicate a Santonian age (CHRISTENSEN, 1994), but the inoceramids are partially of Coniacian age (MALCHUS *et al.*, 1994). The formation has yielded numerous vertebrate fossils, including shark and fish teeth (LERICHE, 1929; HERMAN, 1975), but also turtle, mosasaur and pliosaurid fragmentary remains (DOLLO, 1904, 1909; BARDET & GODEFROIT, 1995). Dinosaurs are also represented at Lonzeée: *Megalosaurus lonzeensis* DOLLO, 1904 is based on a single theropod ungual phalanx and *Craspedodon lonzeensis* DOLLO, 1883, on three ornithischian teeth. In the original description of *Craspedodon*, DOLLO (1883) identified *Craspedodon* as an ornithopod dinosaur: he highlighted the close resemblance of its teeth with those of *Iguanodon*, but also listed the differences between the two taxa. All the subsequent authors followed Dollo's opinion and regarded *Craspedodon* as an ornithopod (e.g. LAPPARENT, 1955; ROMER, 1956; STEEL, 1969; NORMAN & WEISHAMPEL, 1990; PEREDA SUBERBIOLA & SANZ, 1999; NORMAN, 2004).

The teeth attributed to *Craspedodon lonzeensis* are re-examined in the present work because it appeared to us that previous authors have not correctly established their phylogenetic affinities. Indeed, we propose that these teeth should belong to some neoceratopsian, rather than to an ornithopod dinosaur.

Abbreviations

IMM: Inner Mongolia Museum (Hohhot, P.R. China); IRSNB: Institut royal des Sciences naturelles de Belgique (Brussels, Belgium); TsNIGRI: Chernyshev's Central Museum of Geological Exploration (St Petersburg, Russia); UBB: Universitatea din Babes-Bolyai (Cluj, Romania).

2. Description

The studied material consists of three isolated teeth. IRSNB R59 is the smallest (Fig. 2 A-C). Its long and robust root is nearly completely preserved. A longitudinal groove is developed on both its mesial and distal sides, giving the root somewhat of an hourglass shape in cross-section. In ornithischian dinosaurs, the presence of such grooves suggests the organisation of the teeth into dental batteries: the marginal portions of the crowns of the adjacent teeth fitted into these grooves, as observed in Iguanodontia (OSTROM, 1961; NORMAN, 1980, 1986, 2002) and Neoceratopsia (HATCHER *et al.*, 1907; BROWN & SCHLAIKJER, 1940). The tip of the root is notched by a well-developed elliptical flattened facet, which marks

the contact with the crown of the tooth from the next generation in the dental battery (Fig. 2C). In *Iguanodontia* and basal *Neoceratopsia*, the replacement teeth of both the maxillary and dentary batteries contact the lingual side of the functional teeth. In IRSNB R59, this contact facet is developed on the same side as the wear surface of the crown. This suggests that IRSNB R59 is a maxillary tooth: in *Iguanodontia* and *Neoceratopsia*, wear surfaces develop on the lingual side of maxillary teeth and on the labial side of dentary teeth. In mesial and distal views, the root of IRSNB R59 looks semi-lunate, with a convex labial side and a straighter lingual side (Fig. 2B). There is no distinct angulation between the root and the crown: the enamelled side of the crown appears in continuity with the convex labial side of the root, in mesial and

distal views. The crown of IRSNB R59 is heavily worn. Its lingual side is devoid of enamel. The wear surface is distinctly oblique in relation to the longitudinal plane of the tooth, forming a 60° angle with the enamelled side of the crown, and nearly reaches the base of the crown. The enamelled labial side of the crown bears a strong longitudinal primary ridge, placed slightly eccentrically and confluent with a very strong and oblique basal cingulum (Fig. 2A). The enamelled surface of the ridge is very rough. The primary ridge and the cingulum are confluent and limit two deep and unequal U-shaped indentations, or 'pockets', which form the side portions of the enamelled surface of the crown and are marked by a series of secondary ridges.

The details of the crown are better preserved in

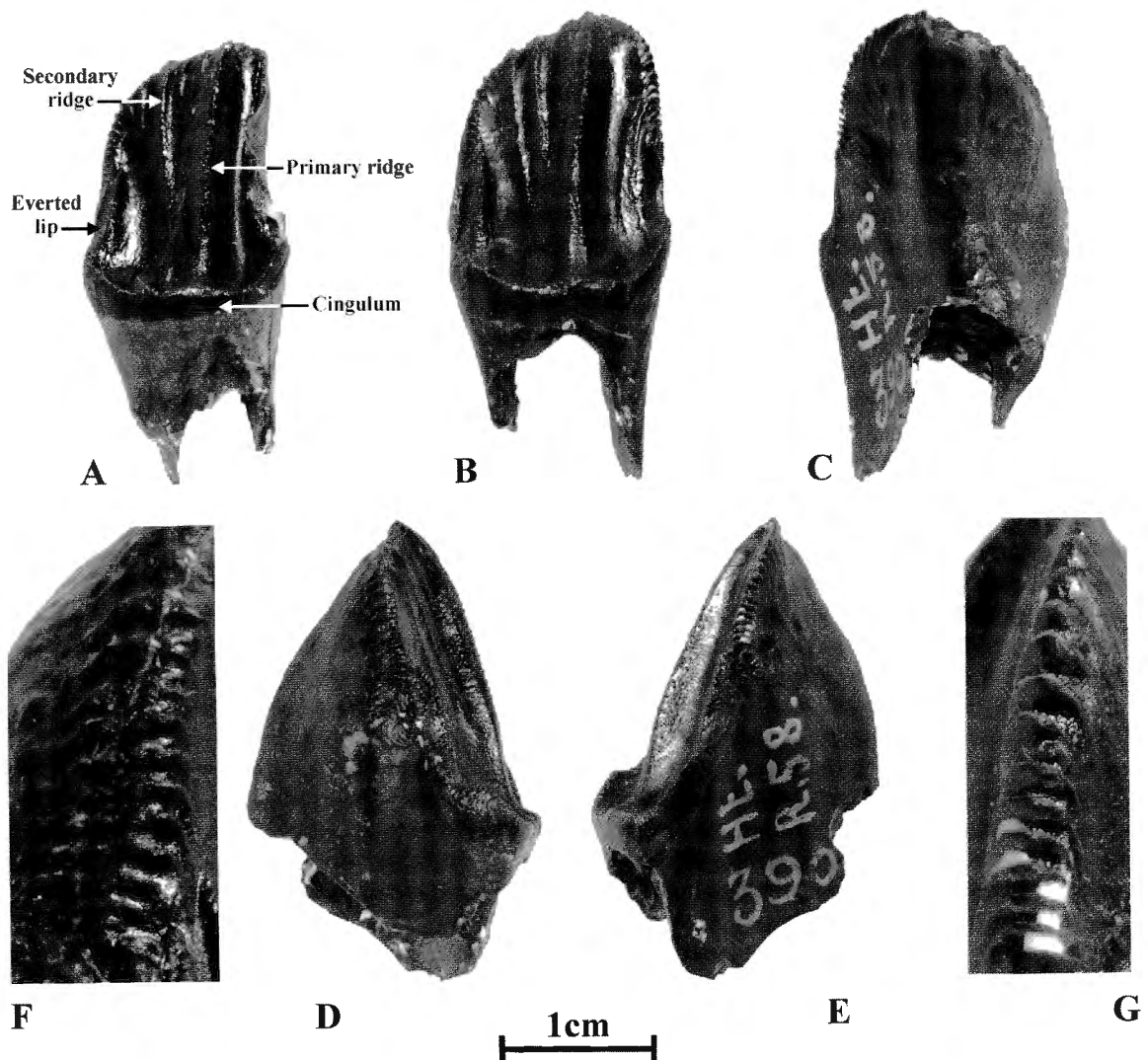


Fig. 3 — Presumed left dentary teeth of *Craspedodon lonzeensis* (A: IRSNB R105; B-G: IRSNB R58), from the Upper Cretaceous of Loncée. A-B: lingual views; C: labial view; D: ?distal view; E: ?mesial view; F: detail of the ?distal creulations; G: detail of the ?mesial creulations.

IRSNB R58 (Fig. 3 B-G) and IRSNB R105 (Fig. 3A), which are larger than IRSNB R59 and completely unworn. The root of both specimens is broken off, so it is not possible to assess with confidence whether these are maxillary or dentary teeth. However, some differences exist with the crown of IRSNB R59, suggesting that they could be dentary teeth: the longitudinal ridge on the enamelled side of the crown is not completely confluent with the cingulum, but is slightly set back from the cingulum, which consequently forms a continuous ridge at the base of the enamelled side. The cingulum is less oblique than in IRSNB R59 and the two 'pockets' consequently look less asymmetrical. Such differences between maxillary and dentary teeth can be observed, for example, in *Leptoceratops* (see BROWN, 1914, figs 2 and 6). The enamelled side of the crown is ovate, with a 'height / maximum width' ratio = 1.53 in IRSNB R58. Secondary ridges are developed on both sides of the longitudinal primary ridge of IRSNB R58 and IRSNB R105: one on the smaller 'pocket', three or four on the larger 'pocket' (Figs 3A-B). They start from the upper part of the edge of the crown and run obliquely toward the base of the crown, but never reach it. Some secondary ridges fuse with the primary ridge. Above the cingulum, both the mesial and distal edges of the enamelled side form an everted lip, limited by a prominent and rough vertical ridge on the enamelled side of the crown, as if the edge of the crown had been pinched inward. The upper part of the edge of the crown bears distinct denticles. They form simple tongue-shaped structures along the edge of the smaller 'pocket' (Figs 3E, 3G). On the other hand, each denticle forms an elongated and curved ledge, which wraps around the edge of the larger 'pocket' of the crown (Figs 3F, 3D). The denticles do not form distinct mammillations, such as those observed in advanced Iguanodontia (NORMAN, 2004). The opposite side of the crown is very convex both vertically and horizontally and forms a bulbous buttress against which the enamelled side of the crown rests (Fig. 3C). This side has a dentine surface, but in some places enamel extends beyond the crown edges.

3. Discussion

Is *Craspedodon* an Iguanodontia or a Neoceratopsia?

In the original description of the material, DOLLO (1883) identified *Craspedodon* as an Ornithopoda on the basis of three characters: the rounded apex in labial/lingual view, the presence of ridges ('crêtes') and the presence of denticles ('dentelures'). But these characters are

not diagnostic for ornithopods, because they can be observed in other ornithischian lineages. Dollo's opinion was followed by all subsequent authors, who referred *Craspedodon* to Iguanodontidae (e.g. LAPPARENT, 1955; ROMER, 1956; STEEL, 1969), Iguanodontia incertae sedis (NORMAN & WEISHAMPEL, 1990; PEREDA SUBERBIOLA & SANZ, 1999), or Iguanodontoidea (NORMAN, 2004). STEEL (1969, p.17) even hypothesized that *Iguanodon hilli* NEWTON, 1892, based upon a tooth from the Totternhoe Stone (Lower Chalk) of Hitchin (Hertfordshire, England), is possibly referable to the genus *Craspedodon*. However, none of these authors argued or discussed their opinion.

When comparing *Craspedodon* teeth with those belonging to the different ornithischian groups, we immediately noticed their striking resemblance with basal neoceratopsian teeth, and particularly with those of *Protoceratops hellenikorhinus* that we had at hand (Fig. 2 D-F), and with TsNIGRI 552/12457, one tooth in the type material of *Turanoceratops tardabilis* NESSOV & KAZNYSHKINA, 1989 (Fig. 2 G-I). If the dental characters used by YOU & DODSON (2003) in their phylogenetic study of Neoceratopsia are applied to the teeth of *Craspedodon*, seven characters support a nested position of this genus among neoceratopsians: maxillary and dentary tooth crown ovate in lateral view (character 103); roots with anterior and posterior grooves (character 104); enamel restricted to one side of the teeth (character 107); median primary ridge on both maxillary and dentary teeth (character 108); primary ridge offset, caudally for maxillary teeth and rostrally for dentary teeth (character 109); primary ridge prominent on maxillary (character 110) and dentary teeth (character 111).

However, all of these characters can also be observed among Iguanodontia. Even though the enamelled side of the crown is lozenge-shaped in hadrosauroids, it is ovate in several Iguanodontia (*Dryosaurus*, *Iguanodon*, *Zalmoxes*...; see Figs 4A-B and 5). The shape of the roots with anterior and posterior grooves is similar in hadrosauroids (*sensu* SERENO, 1998: all hadrosauriforms closer to *Parasaurolophus* than to *Iguanodon*), which have developed dental batteries. The complete absence of enamel on one side of the crown characterises all the hadrosaurids (NORMAN, 1990). This character is also observed in most of the other representatives of the hadrosauroid clade: *Altirhinus* (NORMAN, 1998), *Proactrosaurus* (NORMAN, 2002), *Bactrosaurus* (GODEFROIT *et al.*, 1998), *Gilmoresaurus* (pers. obs.), *Shuangmiosaurus* (YOU *et al.*, 2003), *Telmatosaurus* (pers. obs.), and *Penelopognathus* (GODEFROIT *et al.*, 2005). The development of a primary ridge on both the maxillary and dentary teeth is also widely distributed

among hadrosauroids; in basal members of this clade, the ridge is also asymmetrically placed on the enamelled side of the crown (NORMAN, 1998, 2002; GODEFROIT *et al.*, 2005; Fig. 4 C-D). Therefore, on the basis of these characters, it cannot be decided whether *Craspedodon* is a Neoceratopsia or an Iguanodontia (a basal member of the hadrosauroid clade, in this case).

Nevertheless, additional characters rather speak for neoceratopsian affinities for the teeth of *Craspedodon*. The most important character is the profile of the tooth in mesial or distal view. In *Craspedodon* and most neoceratopsians (excluding *Chaoyangsaurus* and *Archaeoceratops*; see below), the side of the crown that is not covered with enamel is very convex vertically and bulbous. In all Iguanodontia, on the other hand, this

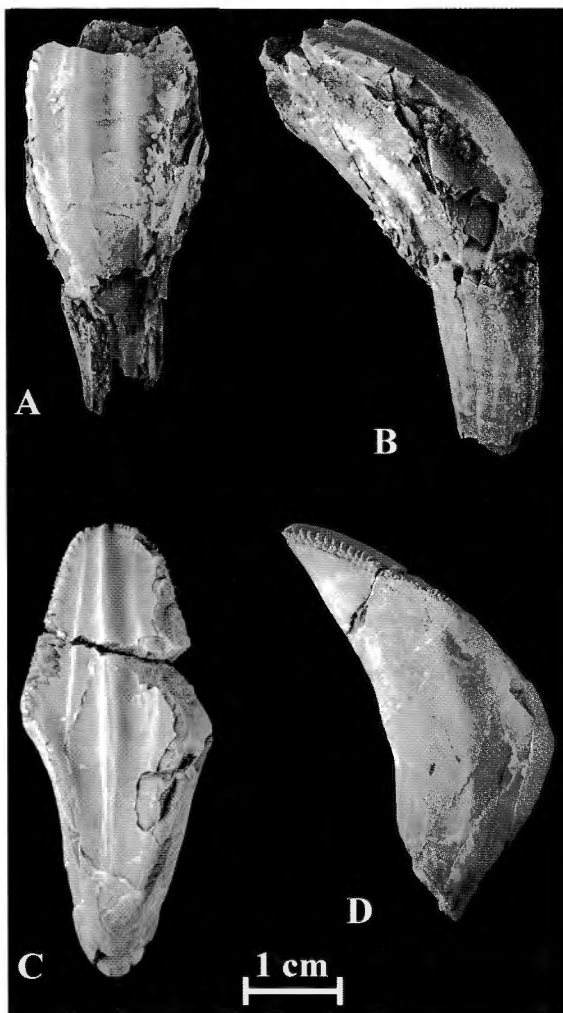


Fig. 4 — Right dentary tooth of *Iguanodon* sp. (A-B: IRSNB R232), from the Lower Cretaceous of Bernissart (Belgium) and right dentary tooth of *Penelopognathus weishampeli* (C-D: IMM 2002-BYGB-1), from the Lower Cretaceous of Qiraga (Inner Mongolia, P.R. China). A and C: lingual views; B and D: mesial views.

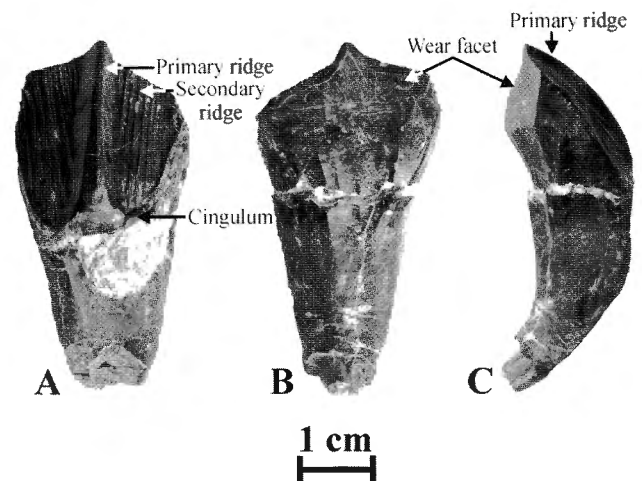


Fig. 5 — Dentary tooth of *Zalmoxes shqiperorum* UBB NVZ1-43a, from the Upper Cretaceous of Nalati-Vad (Hateg Basin, Romania). A: lingual view; B: labial view; C: ?mesial/distal view.

side is concave, roughly parallel to the enamelled side of the crown. The important development of a basal cingulum and associated indentations or 'pockets' on the enamelled side of the crown is also reminiscent of the condition observed in advanced neoceratopsians. Among Iguanodontia, a basal cingulum and associated indentations have only been described in *Zalmoxes* (Fig. 5) and *Rhabdodon* (PINCEMAILLE, 1997), but they are, in any case, less clearly developed than in *Craspedodon* and neoceratopsians. The development of the secondary ridges also seems informative. In *Craspedodon* and non-ceratopsid Neoceratopsia, the secondary ridges start from the apex of the crown and do not reach the base of the crown. In Iguanodontia, on the other hand, secondary ridges start from the base of the crown; they reach the marginal denticles in basal forms (*Zalmoxes*), but stop below it in most advanced forms (*Altirhinus*, *Penelopognathus*, *Probactrosaurus*, *Bactrosaurus*). *Camptosaurus* is the only ornithomimid in which the secondary ridges start from the apical edge, but end prior to the base of the crown (CHINNERY *et al.*, 1998), as observed in *Craspedodon*.

It can therefore be concluded that *Craspedodon* displays several dental features that can equally be observed in neoceratopsians and in iguanodontians. However, other characters (shape of the tooth in mesial or distal view, strong development of cingulum and indentations, secondary ridges that do not reach the base of the crown) are more compatible with neoceratopsian affinities for *Craspedodon*. Of course, it cannot be excluded that *Craspedodon* is a very basal hadrosauroid that developed autapomorphies convergent with

the condition in neoceratopsians. However, the most parsimonious hypothesis is to consider these enigmatic teeth as belonging to some neoceratopsian dinosaur.

Craspedodon within Neoceratopsia

Below, we discuss the main characters observed on the teeth of *Craspedodon*. We show that all are consistent with the hypothesis that they belong to a neoceratopsian dinosaur and we precise the phylogenetic position of *Craspedodon* within Neoceratopsia. Figure 6 shows the phylogenetic relationships among the main basal neoceratopsians (simplified from YOU & DODSON, 2003).

Tooth enamel distribution - Primitively in ornithischians, the enamel is distributed on both sides of the crowns (YOU & DODSON, 2003: character 107). This condition is retained in the basal neoceratopsians *Chaoyangsaurus* and *Liaoceratops*. In all the other neoceratopsians, the enamel is absent on the lingual side of the maxillary teeth and on the labial side of the dentary teeth (CHINNERY & WEISHAMPEL, 1998; SERENO, 2000; MAKOVICKY, 2001; YOU & DODSON, 2003), as observed in the teeth referred to *Craspedodon*. The corollary of this condition is the development of a single well-defined triturating surface on the side of the crown that is not covered with enamel.

Shape of the tooth root - Primitively in ornithischians, the root of the cheek teeth is cylindrical (YOU & DODSON, 2003: character 104). This condition is apparently retained in *Chaoyangsaurus* and *Liaoceratops*. (MAKOVICKY, 2001; YOU & DODSON, 2003). Longitudinal grooves are developed on the mesial and distal sides of the tooth roots in all the other Neoceratopsia, including *Craspedodon*.

Number of tooth roots - Primitively in ornithischians, the root of the cheek teeth is single and long (YOU & DODSON, 2003: character 113). This condition is retained in *Craspedodon* and also in most basal neoceratopsians, leptoceratopsids, and protoceratopsids. In *Craspedodon* and *Protoceratops*, a well-developed surface at the base of the root indicates the contact with the crown of the succeeding tooth (Figs 2C, 2F). Because of the long root, the succeeding tooth is far removed from the crown of the functional tooth, leading to a considerable gap between the functional end of this latter tooth and the eruption of the next one. In ceratopsids, on the other hand, the root of each cheek tooth becomes transversely bifurcated by the root dividing and spreading over the crown of the succeeding tooth. The crown of the succeeding tooth is therefore not so far removed from that of the functional tooth, leading to a more even wear surface on the whole dental battery (BROWN & SCHLAIKJER, 1940).

Shape of the tooth crown in labial or lingual view - Primitively in ornithischians, the tooth crown is pennate or radiate in labial or lingual view (YOU & DODSON, 2003: character 103). Among Neoceratopsia, this condition is preserved in *Chaoyangsaurus*. In *Liaoceratops* and *Archaeoceratops*, the dentary teeth keep the plesiomorphic condition, whereas the maxillary teeth are ovate in labial / lingual view. In all the other neoceratopsians, both the dentary and maxillary teeth are ovate in labial / lingual view (SERENO, 2000; MAKOVICKY, 2001; YOU & DODSON, 2003), as is probably the case in *Craspedodon*.

Shape of the tooth crown in mesial or distal view - Primitively in ornithischians, the maxillary and dentary teeth are asymmetrical in mesial and distal views, with a convex labial side, and a flattened or vertically concave lingual side (HUNT & LUCAS, 1994; GODEFROIT & CUNY, 1997). In basal ceratopsian teeth, including those of Psittacosauridae, the non-enamelled (or less-enamelled) side of the crown is slightly convex in both dorsoventral and mesiodistal directions. However, at the base of the crown, the mesiodistal diameter largely

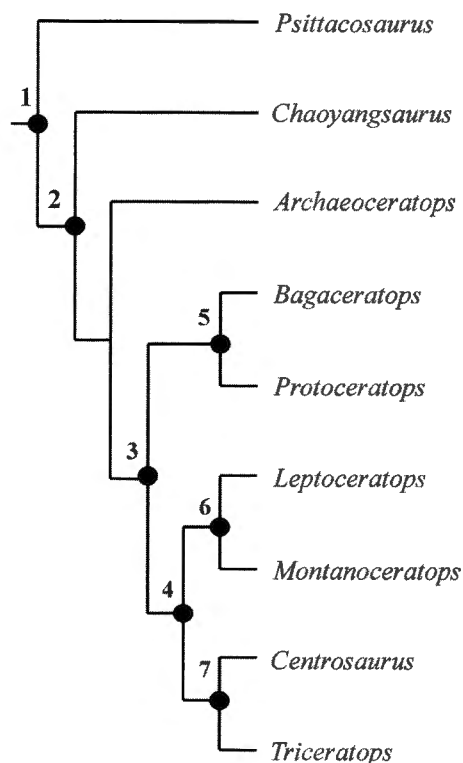


Fig. 6 — Simplified phylogeny of Ceratopsia (modified from YOU & DODSON, 2003). 1: Ceratopsia; 2: Neoceratopsia; 3: Coronosauria; 4: Ceratopsioidea; 5: Protoceratopsidae; 6: Leptoceratopsidae; 7: Ceratopsidae.

exceeds the labiolingual diameter. This condition is retained in *Chaoyangsaurus* (ZHAO *et al.*, 1999) and apparently in *Archaeoceratops* (DONG, pers. comm.). In all the other neoceratopsians, the lingual side of the maxillary teeth and the labial side of the dentary teeth are very convex vertically and bulbous. However, in protoceratopsids, the mesiodistal diameter of the base of the crown still exceeds slightly the labiolingual diameter. In leptoceratopsids and ceratopsids, the labiolingual diameter at the base of the crown largely exceeds the mesiodistal diameter, as also observed in *Craspedodon* (HATCHER *et al.*, 1907; BROWN, 1914).

Tooth occlusion direction - Primitively in Marginocephalia, the tooth occlusion pattern is oblique sheer (SERENO, 1986; MARYAŃSKA, 1990; YOU & DODSON, 2003: character 102). This condition, observed in *Craspedodon*, is retained in basal neoceratopsians (ZHAO *et al.*, 1999; YOU & DODSON, 2003) and protoceratopsids (MARYAŃSKA & OSMÓLSKA, 1975). In ceratopsids, teeth occlude at a more vertical angle, with an apical plane orientation more than 45° from the primary axis of the root (SERENO, 2000). In *Leptoceratops* and *Montanoceratops*, teeth also occlude at a vertical angle, but dentary teeth have a horizontal shelf on the labial side (CHINNERY & WEISHAMPEL, 1998; MAKOVICKY, 2001; YOU & DODSON, 2003).

Development of a cingulum and of deep indentations on the cheek teeth - Primitively in ornithischians, there is no cingulum at the base of the teeth and there is no trace of deep indentations, or 'pockets'. This condition is retained in *Chaoyangsaurus* (ZHAO *et al.*, 1999), *Archaeoceratops* (YOU & DODSON, 2003) and *Liaoceratops* (XU *et al.*, 2002). A basal cingulum is developed in more advanced neoceratopsians and deep indentations are consequently limited, on the enamelled side of the crown, by the primary ridge and the cingulum. In protoceratopsids (pers. obs.), the cingulum is still poorly developed on both the lingual side of the dentary teeth and on the labial side of the maxillary teeth. The primary ridge therefore looks confluent with the cingulum. In leptoceratopsids and *Craspedodon*, the cingulum is much better developed on the dentary teeth and the primary ridge is set back from the cingulum, which forms a continuous ridge at the base of the lingual side of the crown. On the maxillary teeth, the cingulum and primary ridge are still confluent (see BROWN, 1914, figs 2 and 6). In ceratopsids, the primary ridge is set back from the cingulum on both the dentary and maxillary teeth (character 106; see HATCHER *et al.*, 1907, figs 42-46).

Development and position of primary ridges - Primitively in Marginocephalia, there is no prominent primary ridge on one side of the cheek tooth crowns

(character 108). The presence of a primary ridge on the labial side of the maxillary teeth is observed in all neoceratopsians except *Chaoyangsaurus* and *Liaoceratops* (ZHAO *et al.*, 1999; YOU & DODSON, 2003). The primary ridge, when present, is offset distally on the maxillary teeth (SERENO, 2000; YOU & DODSON, 2003). The presence of a primary ridge on both the labial side of the maxillary teeth and on the lingual side of the dentary teeth, the condition seen in *Craspedodon*, is regarded as a synapomorphy shared by leptoceratopsids, protoceratopsids, and ceratopsids (SERENO, 2000; MAKOVICKY, 2001). When present, the primary ridge is offset mesially on the dentary teeth (SERENO, 2000; YOU & DODSON, 2003).

Development of secondary ridges - Secondary ridges on the enamelled (or most enamelled) side of the crowns, starting from the apical part of the edge but not reaching the cingulum, as observed in *Craspedodon*, are also present in *Psittacosaurus* (pers. obs.), basal neoceratopsians (ZHAO *et al.*, 1999; YOU & DODSON, 2003), protoceratopsids (BROWN & SCHLAIKJER, 1940; MARYAŃSKA & OSMÓLSKA, 1975), and leptoceratopsids (BROWN, 1914). In ceratopsids, on the other hand, secondary ridges are rudimentary or absent (YOU & DODSON, 2003: character 112; SERENO, 2000).

With such a low number of characters, it is of course not the purpose of the present paper to propose a new phylogenetic analysis of Ceratopsia. However, the analysis of the dental characters discussed above provides the opportunity to go further in the determination of the phylogenetic affinities of *Craspedodon*. With Coronosauria (the most recent common ancestor of *Protoceratops* and *Triceratops*, and all of its descendents: SERENO, 1998), *Craspedodon* shares the following synapomorphies: the enamel is absent on the lingual side of the maxillary teeth and nearly completely absent on the labial side of the dentary teeth, longitudinal grooves are developed on the mesial and distal sides of the tooth roots, both the dentary and maxillary teeth are ovate in lateral view, a cingulum and deep indentations are developed on the cheek teeth, and a primary ridge is well developed on both the maxillary and dentary teeth. YOU & DODSON (2003, 2004; *contra* e.g. SERENO, 2000; MAKOVICKY, 2001) distinguish two clades within Coronosauria: the Asian Protoceratopsidae (Coronosauria closer to *Protoceratops* than to *Triceratops*) and the essentially North American Ceratopsioidea (Coronosauria closer to *Triceratops* than to *Protoceratops* and including Leptoceratopsidae and Ceratopsidae). The teeth of *Craspedodon* appear more derived than those of Protoceratopsidae and share the following ceratopsoid characters: the labiolingual

diameter at the base of the crown largely exceeds the mesiodistal diameter, the cingulum is very developed on the dentary teeth and the primary ridge is set back from the cingulum, which forms a continuous ridge at the base of the lingual side of the crown. However, the teeth of *Craspedodon* do not display any leptoceratopsid or ceratopsid synapomorphies. The tooth occlusion direction is not vertical-notch sheer as in leptoceratopsids. Contrary to ceratopsids, at least the maxillary teeth of *Craspedodon* are not double-rooted, tooth occlusion is not vertical, the primary ridge is not set back from the cingulum on the maxillary teeth, and the secondary ridges are not rudimentary or absent. We can therefore conclude that *Craspedodon lonzeensis* is probably a basal representative of the ceratopsoid clade (*sensu* YOU & DODSON, 2003, 2004). The question remains to know whether *Craspedodon lonzeensis* is a valid taxon or must best be regarded as a *nomen dubium*. Autapomorphic characters would include the asymmetrical morphology of the denticulations on the edges of the crown and the lateral edges forming everted lips, limited by a prominent and rough vertical ridge on the enamelled side of the crown. However, MARYAŃSKA & OSMÓLSKA (1975) observed that "The shape of the protoceratopsid tooth and the number and the character of the smaller, lateral ribs are variable even in the adult individuals and vary accordingly to the place which the tooth occupies in the jaw. For these reasons, we recommend that isolated protoceratopsid teeth should not be used as a basis for the erection of new taxa." Moreover, little attention has been paid to date to the detailed morphology of the teeth in ceratopsoid dinosaurs. For that reason, we prefer to shelve this question, pending the possibility of discovering more complete *Craspedodon* material in the future and the detailed study of the crown ornamentation in ceratopsoids. The most interesting result of this study is that, in any case, ceratopsoids were apparently present in Europe by Coniacian-Santonian times. This is in fact the only record of neoceratopsian dinosaurs in Europe. DEPÉRET (1900) tentatively reported ceratopsian remains from the Upper Cretaceous of the Saint-Chinian area in southern France, but NOPCSA (1929) subsequently demonstrated that this was based on a misinterpretation of ankylosaur bones. Later, ANTUNES & PAIS (1978) and ANTUNES & BROIN (1988) cited but did not describe a possible ceratopsian from the Upper Cretaceous of Beira Litoral, Portugal; this unconfirmed identification is considered doubtful (GALTON, 1994).

Palaeobiogeography of neoceratopsian dinosaurs

YOU & DODSON (2003) propose a very simple view of Coronosauria palaeobiogeography, with the recognition of two separate clades in Asia (Protoceratopsidae) and North America (Ceratopsioidea). This scenario implies a single dispersal event from Asia to western North America via the Bering land bridge, probably during the early Late Cretaceous. Nevertheless, the situation appears to be more complicated. Recent discoveries of isolated teeth have pushed back the first occurrence of neoceratopsians in eastern North America to the middle-late Aptian (CHINNERY *et al.*, 1998) and in western North America to the middle or late Albian (CIFELLI *et al.*, 1997; KIRKLAND *et al.*, 1997; CHINNERY *et al.*, 1998). Moreover, ceratopsoids probably had a much larger palaeogeographic distribution: besides North America, ceratopsoid fossils have also been described in the Coniacian-Santonian of western Europe (this paper) and in the Upper Turonian of Uzbekistan (NESSOV & KAZNYSHKINA, 1989).

The neoceratopsian clade most likely originated in Asia, because this is where its sister group, Psittacosauridae, and its basal forms, *Chaoyangsaurus*, *Liaoceratops* and *Archaeoceratops*, are distributed. If the neoceratopsian phylogeny used by YOU & DODSON (2003, 2004) is correct, Protoceratopsidae were present in Asia and flourished there until the late Campanian. In the current state of our knowledge, no neoceratopsian is known from Maastrichtian deposits in Asia. On the other hand, Ceratopsioidea (*sensu* YOU & DODSON, 2003) spread over Laurasia, giving rise to the ceratopsids known from the Campano-Maastrichtian of western North America. The presence of neoceratopsians both in western and eastern North America by Aptian-Albian time can easily be explained by one or more dispersal events across the Bering land bridge, which has been determined to be in place from the 'middle' Cretaceous onward (RUSSELL, 1993; CIFELLI *et al.*, 1997). At the same time, intermittent land bridges also connected Asia and northern Europe, separated by the Turgai Straits from the end of the Middle Jurassic, allowing faunal exchanges between the two regions (RUSSELL, 1993; SMITH *et al.*, 1994). Ceratopsoids could disperse into northern Europe during this short period. The Turgai Straits apparently reopened from the Cenomanian onward, isolating northern Europe from Central Asia during the Late Cretaceous (SMITH *et al.*, 1994). A migration of ceratopsoid dinosaurs from eastern North America into Europe is very unlikely, because both regions were separated by a proto-North Atlantic Ocean during most of the Cretaceous. A land bridge probably connected southern Europe and North

America by Berriasian-Valanginian time, well before land connections were established between Asia and Europe, on the one hand, and Asia and North America, on the other hand (SMITH *et al.*, 1994).

It can therefore be concluded that Europe was isolated from Asia and North America during the Late Cretaceous (LE LOEUFF, 1991; SMITH *et al.*, 1994), even if a transatlantic dispersal route has been recently suggested, probably later during the Late Cretaceous, based on the discovery of the marsupial *Maastrichtidelphys* in the Maastrichtian of The Netherlands (MARTIN *et al.*, 2005). Neoceratopsians probably migrated from Asia into Europe during the Aptian-Albian, when intermittent land bridges were established across the Turgai Straits. Nevertheless, it must be noted that no ceratopsians have so far been reported from the Aptian-Albian deposits of Europe, although the European dinosaur record for that time span is not that bad, with notably a fairly diverse record from the Cambridge Greensand in England, but also from other localities in England, France and Spain (see WEISHAMPEL *et al.*, 2004). An Aptian-Albian migration also implies a relatively long ghost lineage for neoceratopsians in Europe, of more than nine millions years, between their migration toward Europe until their attested presence in the Loncée Member. This long ghost lineage duration perfectly reflects the very fragmentary state of our knowledge about Late Cretaceous terrestrial ecosystems in Europe prior to the Campanian (BUFFETAUT *et al.*, 1981; LE LOEUFF, 1991; WEISHAMPEL *et al.*, 2004). Although neoceratopsians flourished in Asia during the Campanian and in western North America during the Campano-Maastrichtian, they are apparently absent from Campano-Maastrichtian ecosystems in Europe, which are yet well represented in southern France (LE LOEUFF, 1991; ALLAIN & PEREDA SUBERBIOLA, 2003), northern Spain (ASTIBIA *et al.*, 1999), and Romania (GRIGORESCU, 2003).

Acknowledgements

The photographic work was made by T. Hubin and W. Miseur. P. Barrett, E. Buffetaut, and X. Pereda Suberbiola read an earlier version of the manuscript and made many helpful comments. The work of O. L. at the IRSNB is financially supported by the Belgian Federal Science Policy Office (Research Project MO/36/016).

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Typescript submitted: July 16, 2006

Revised typescript received: April 4, 2007

