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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**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 Ceratopsidae (sensu YOU & DODSON, 2003, 2004) 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.
exploited until 1914 because of its colouring properties. The belemnites at Lonzée 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 Lonzée: 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 enameled 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 enameled side of the crown, and nearly reaches the base of the crown. The enameled 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 enameled 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 enameled surface of the crown and are marked by a series of secondary ridges.

The details of the crown are better preserved in

![Diagram of Craspedodon lonzeensis](Image)

Fig. 3 — Presumed left dentary teeth of *Craspedodon lonzeensis* (A: IRSNB R105; B-G: IRSNB R58), from the Upper Cretaceous of Lonzee. A-B: lingual views; C: labial view; D: ?distal view; E: ?mesial view; F: detail of the ?distal crenulations; G: detail of the ?mesial crenulations.
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 (‘crétes’) 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 Iguanodontoidia (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 helenikorhinus* that we had at hand (Fig. 2 D-F), and with TsNIgRI 552/12457, one tooth in the type material of *Turanceratops tarkibilies* 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 hadrosaurids, 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 hadrosaurids (*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 hadrosaur clade: *Altirhinus* (Norman, 1998), *Probactrosaurus* (Norman, 2002), *Bactrosaurus* (Godfrey et al., 1998), *Gilmoreosaurus* (pers. obs.), *Shuangmiosaurus* (You et al., 2003), *Telmatosaurus* (pers. obs.), and *Penelopognathus* (Godfrey 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 hadrosaurid 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 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* (Pincaemaille, 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 ornithopod 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 hadrosaurid 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 precisé the phylogenetic position of Craspedodon within Neoceratopsia. Figure 6 shows the phylogenetic relationships among the main basal neoceratopsians (simplified from YOU & DOSDON, 2003).

**Tooth enamel distribution** - Primitively in ornithischians, the enamel is distributed on both sides of the crowns (YOU & DOSDON, 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 & DOSDON, 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 & DOSDON, 2003: character 104). This condition is apparently retained in Chaoyangsaurus and Liaoceratops. (MAKOVICKY, 2001; YOU & DOSDON, 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 & DOSDON, 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 pinnate or radiate in labial or lingual view (YOU & DOSDON, 2003: character 103). Among Neoceratopsia, this condition is preserved in Chaoyangsaurus. In Liaoceratops and Archaeoceratops, the dentary teeth keep the pleisiomorphic 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 & DOSDON, 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

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Fig. 6 — Simplified phylogeny of Ceratopsia (modified from YOU & DOSDON, 2003). 1: Ceratopsia; 2: Neoceratopsia; 3: Coronosauria; 4: Ceratopsoidia; 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 shear (Sereno, 1986; Maryńska, 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 (Maryńska & 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 *Liaoaceratops* (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 *Liaoaceratops* (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; Maryńska & 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 Ceratopia. 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 linguoal 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 shear 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 ceratopsid 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 denticleations 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 protoceratopid 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 where the tooth occupies in the jaw. For these reasons, we recommend that isolated protoceratopid 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 ceratopsid 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 ceratopsids. 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).
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 Lonzée 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