

The skull of *Triceratops* in the palaeontology gallery, Muséum national d'Histoire naturelle, Paris

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ABSTRACT

The specimen of *Triceratops calicornis* Marsh, 1898 exhibited in the gallery of palaeontology in the Muséum national d'Histoire naturelle of Paris consists of a skull lacking the lower jaw, except for the predentary. It was presented in October 1912, when Marcellin Boule was chairman of the Palaeontology department, and registered as MNHN 1912.20. This specimen, long overlooked in the literature, is described herein for the first time. Since its erection by Marsh in 1889, up to 16 species have been referred to the genus *Triceratops*. However, during the last 20 years, our comprehension of the biology and variability of large living tetrapods has called into question the validity of these *Triceratops* species. Although a consensus on this question now seems to emerge, several models have been still discussed recently. The description of MNHN 1912.20 offers an opportunity to discuss these different hypotheses.

KEY WORDS

Dinosauria,
Ceratopsia,
Triceratops,
Paris,
skull,
systematics.

RÉSUMÉ

Le crâne de Triceratops de la galerie de paléontologie du Muséum national d'Histoire naturelle, Paris.

Le spécimen de *Triceratops calicornis* Marsh, 1898 (constitué d'un crâne dépourvu de mâchoire inférieure, à l'exception du prédentaire) de la galerie de paléontologie du Muséum national d'Histoire naturelle de Paris est arrivé en France en octobre 1912 à l'initiative de Marcellin Boule, alors titulaire de la chaire de Paléontologie. Ce spécimen est alors enregistré sous le numéro MNHN 1912.20. Depuis sa création par Marsh en 1889, jusqu'à 16 espèces ont été proposées au sein du genre *Triceratops*. Mais au cours des 20 dernières années, notre compréhension de la biologie et de la variabilité des grands tétrapodes actuels a fortement remis en cause la validité de ces espèces, et si un consensus sur la question est à présent admis, plusieurs hypothèses étaient encore discutées récemment. Ainsi, parallèlement à une description complète du spécimen MNHN 1912.20, le point est fait sur les travaux récents concernant la classification du genre *Triceratops*. Ce crâne, ignoré des études précédentes, devrait désormais être intégré aux futurs travaux sur ce genre.

MOTS CLÉS
Dinosauria,
Ceratopsia,
Triceratops,
Paris,
crâne,
systématique.

INTRODUCTION

Triceratops Marsh, 1889 is one of the favourite dinosaurs for the public, alongside the equally famous contemporary species *Tyrannosaurus rex*. Various reconstructions representing fights between these two potential adversaries have contributed to the fascination raised by the characteristic and unusual morphology of *Triceratops*. However, besides its frequent appearance in the popular media, *Triceratops* is also one of the best documented dinosaurs, both because of its abundance in the fossil record and its generally good state of preservation. To date, about 30 more or less complete skulls are recorded, as well as a significant quantity of postcranial material, although no complete articulated skeleton has been described.

Nevertheless, it is worth noting that this taxon, in spite of its notoriety and the strong interest it raises

among scientists, has posed many problems as to its classification. Since its erection by Marsh in 1889, up to the latest theories, the systematics of the genus *Triceratops* has been constantly revised. Central to this debate is the much discussed question as to the number of species that should be included in it.

Many previous studies have pointed out that the characteristic morphology of *Triceratops* displays a significantly wide range of variation in shape and size. In addition, because of the rarity of juvenile individuals (Goodwin *et al.* 1997, 2006; Goodwin & Horner 2001), this variability has been interpreted in many different ways such as broad species diversity, wide range of intraspecific variability in a single species, or sexual dimorphism (Hatcher *et al.* 1907; Lull 1933; Lehman 1990, 1998; Forster 1996b).

In this context, the re-examination of the specimen of *Triceratops calicornis* Marsh, 1898 of the



FIG. 1. — *Triceratops horridus* Marsh, 1889 (MNHN 1912.20), previously referred to as *Triceratops calicornis* Marsh, 1898; Upper Cretaceous, Lance Creek, Converse County, Wyoming, USA; skull and premaxilla in right anterolateral view.

Muséum national d'Histoire naturelle de Paris (MNHN) is useful as this specimen has never been properly studied, since its presentation in the gallery of palaeontology in October 1912 (Fig. 1).

Beside the complete description of this specimen, one of the goals of this study is to determine its taxonomic assignment in the light of present hypotheses about the systematics of the genus *Triceratops*.

THE SKULL OF *TRICERATOPS CALICORNIS* (MNHN 1912.20)

HISTORY

The acquisition of this skull is due to Marcellin Boule, whose correspondence with Charles Hazelius Sternberg shows a real interest in obtaining a specimen of this taxon. Through this correspondence,

it also appears that several specimens were proposed by C. H. Sternberg before the purchase of this particular one by the MNHN. The refusal of the other specimens was mainly due to financial problems, the sum requested being provided by generous donors.

By combining the information collected in this correspondence and the memoirs of C. H. Sternberg (Sternberg 1985, 1990), the history of the specimen can be reconstructed from its discovery to its arrival in Paris. Discovered in Wyoming in 1911 by the team of C. H. Sternberg and prepared by his son Charles Mortram Sternberg, sale of the skull was proposed to Boule on March 8, 1912. The latter offered \$1000 on March 20, after having rejected another specimen found by Sternberg the preceding summer and finally sold to the Victoria Memorial Museum, Ottawa, Canada. The skull, sent on July 18, 1912,

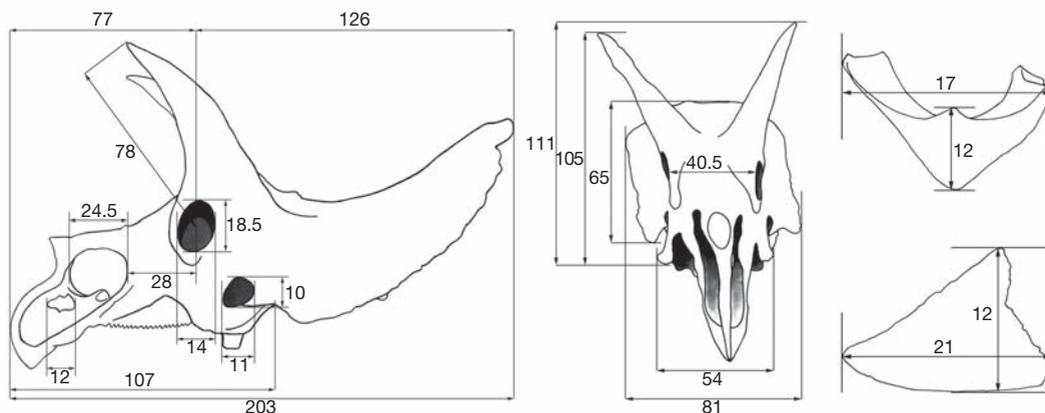


FIG. 2. — *Triceratops horridus* Marsh, 1889; Upper Cretaceous, Lance Creek, Converse County, Wyoming, USA; skull and predeimentary MNHN 1912.20, measurements in cm.

was finally registered at MNHN on October 2, 1912, as 1912.20. The skull is associated with an isolated *Triceratops* horn collected from the same layer (same number: 1912.20).

LOCALITY AND STRATIGRAPHIC DATA

Unfortunately, the data provided by the correspondence between Boule and Sternberg do not allow us to locate precisely the site from which the Paris specimen was extracted: it comes from the area of Lance Creek, in Converse County, Wyoming, from the Lance Formation dated as Maastrichtian (Upper Cretaceous). In fact, this is the main locality where the 16 *Triceratops* species were found, although many other undescribed specimens were also collected in North Dakota, Colorado, Montana, Alberta and Saskatchewan.

DESCRIPTION

Although abundantly restored (mainly for the frill), the skull MNHN 1912.20 is a best preserved specimen and, except for the missing mandible, one of most complete ones. However, this specimen has not been mentioned in the various past and modern studies of *Triceratops*.

With an overall length of more than 2 m (Fig. 2), this specimen represents one of largest skulls of *Triceratops* known so far, but the frill restoration could bias this measurement and is debatable com-

pared to the other described specimens. A significant distortion of skull (due to strong lateral pressure following burial) also biases the measurement of its greatest width, which differs notably from values recorded for other specimens.

Interestingly, the majority of the cranial sutures are not completely closed, thereby allowing, on the one hand, a relatively complete description of the cranial bones (Fig. 3) and, on the other, a conclusion about the age of the individual. Considering Ostrom & Wellnhofer's (1986) conclusion that the lack of sutures between the bones probably indicates an advanced age for an individual, the presence of these sutures in the Paris specimen suggests that this individual had not yet reached maturity.

Some general characters of this skull are: relatively long and particularly robust brow horns with oval section, and with a pronounced forward curvature; the presence of sutured epoccipitals in some areas on the margin of the frill; the presence of significant marks of vascularization on the frill and brow horns; and a large, spherical and slightly downwardly directed occipital condyle.

Rostral (R)

In lateral view, this bone presents a strongly curved profile, yet not hooked, plunging in rostrally from the nasal horn. It is separated from the nasal and

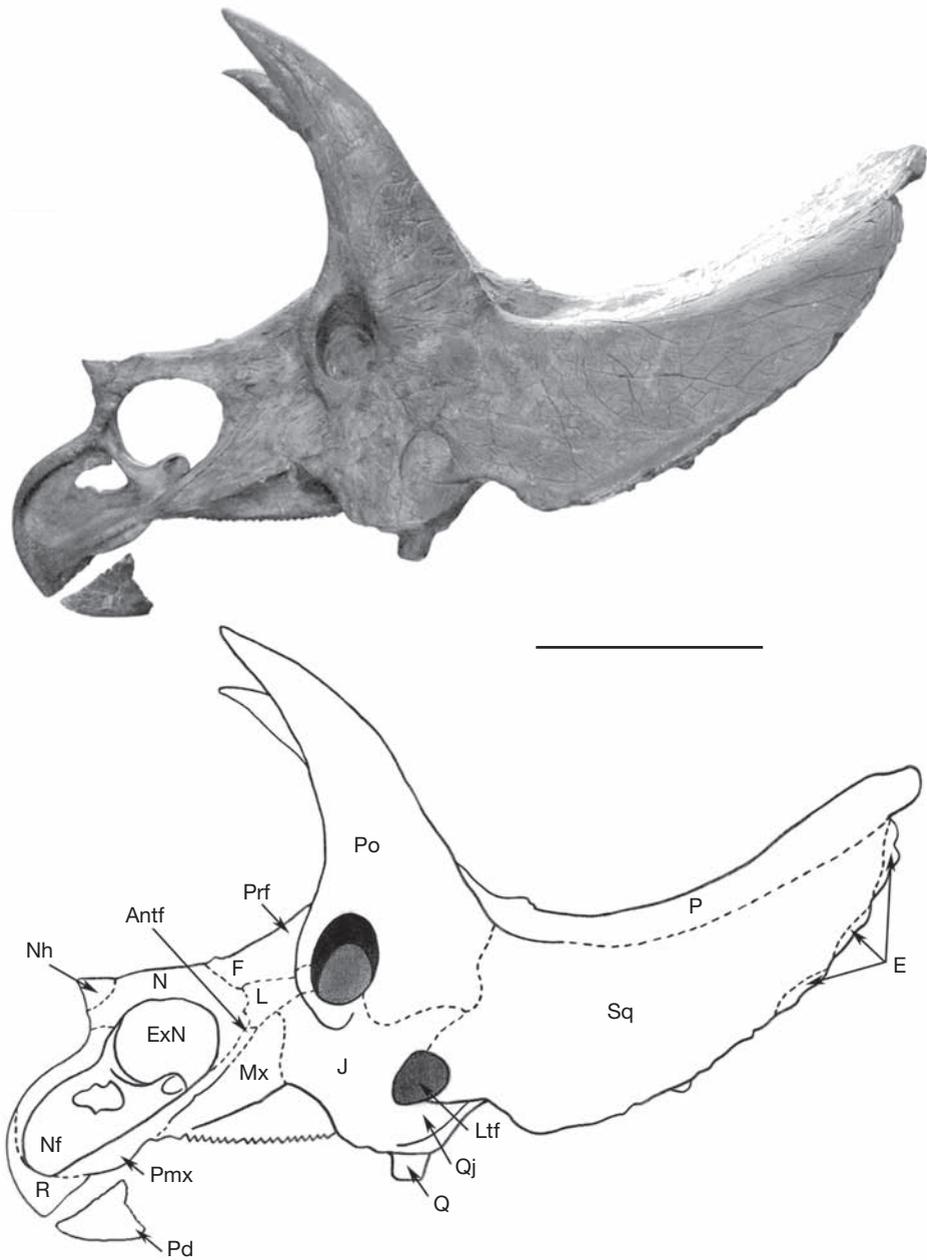


FIG. 3. — *Triceratops horridus* Marsh, 1889; Upper Cretaceous, Lance Creek, Converse County, Wyoming, USA; skull MNHN 1912.20 in left lateral view. Abbreviations: **Antf**, antorbital fenestra; **E**, epoccipital; **ExN**, external nares; **F**, frontal; **J**, jugal; **L**, lachrymal; **Ltf**, lower temporal fenestra; **Mx**, maxilla; **N**, nasal; **Nf**, narial fossa; **Nh**, nasal horn; **P**, parietal; **Pd**, predentary; **Pmx**, premaxilla; **Po**, postorbital; **Prf**, prefrontal; **Q**, quadrate; **Qj**, quadratojugal; **R**, rostral; **Sq**, squamosal. Scale bar: 50 cm.

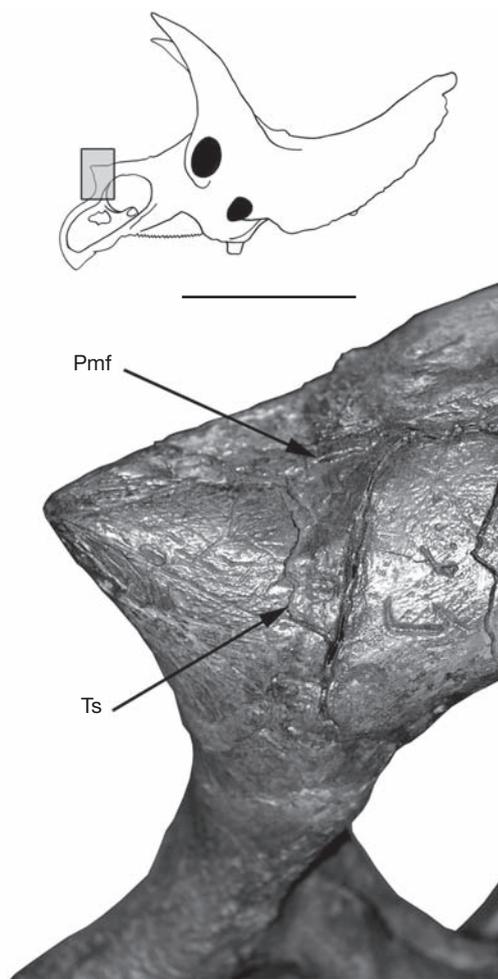


FIG. 4. — *Triceratops horridus* Marsh, 1889; Upper Cretaceous, Lance Creek, Converse County, Wyoming, USA; position and detail of the nasal horn. Abbreviations: **Pmf**, post-mortem fracture; **Ts**, transverse suture. Scale bar: 5 cm.

maxilla by the premaxilla which gives it an S-shaped profile.

Maxilla (Mx)

In lateral view, the maxilla is triangular in shape, its dorsal margin extending dorsally towards the orbit. This bone consists of two portions: a deep, prominent process caudally prolonged in contact with the jugal, and a ventral, more internal portion, with a profile curved towards the outside and 48 tooth positions.

Antorbital fenestra (Anf)

The antorbital fenestra is visible only on the left side of skull, the right part having been covered when the specimen was restored. This fenestra is oval in shape, located along the dorsal margin of the maxilla, and its long axis forms an angle of approximately 45° with the ventral margin of the maxilla.

Nasal (N)

The nasal forms the caudal and dorsal margins of the external nares and supports the median nasal horn (Nh), the origin of which has been discussed by many authors (Ostrom & Wellnhofer 1986; Forster 1996a): either a simple outgrowth of the nasal, or a separate ossification. As regards specimen MNHN 1912.20, the presence of a transverse suture at the base of the horn seems to support the hypothesis of an independent epinasal ossification, although the presence of a well marked furrow passing through the top of the horn could represent the trace of the suture between the two adjacent nasals (Fig. 4). However, this furrow may be a post-mortem fracture, as suggested by the fact that the two halves of the horn it separates are unequal in size (Ostrom & Wellnhofer 1986). This reduced horn projects forwards, forming an angle of about 30° with the ventral margin of the maxilla.

Narial complex of the premaxilla

This consists of the external nares caudally and the structures forming the narial fossa rostrally. The caudal margin of the narial fossa forms a thick strut that runs obliquely from the base of the nasal horn to the zone of contact between the premaxilla and maxilla. A pair of thin rectangular processes projects caudally from the base of the narial strut into the interior of the external nares. These rectangular processes diverge slightly and are deeply excavated laterally at their base by a channel joining the narial fossa. The fossa is thin and fenestrated by a large opening in the cranial portion of the premaxilla.

Frontal (F) / prefrontal (Prf)

The excessive coating applied at the time of restoration of the specimen precludes the clear delineation of the limits between these bones. The rugose surface and strong development of the prefrontal suggest

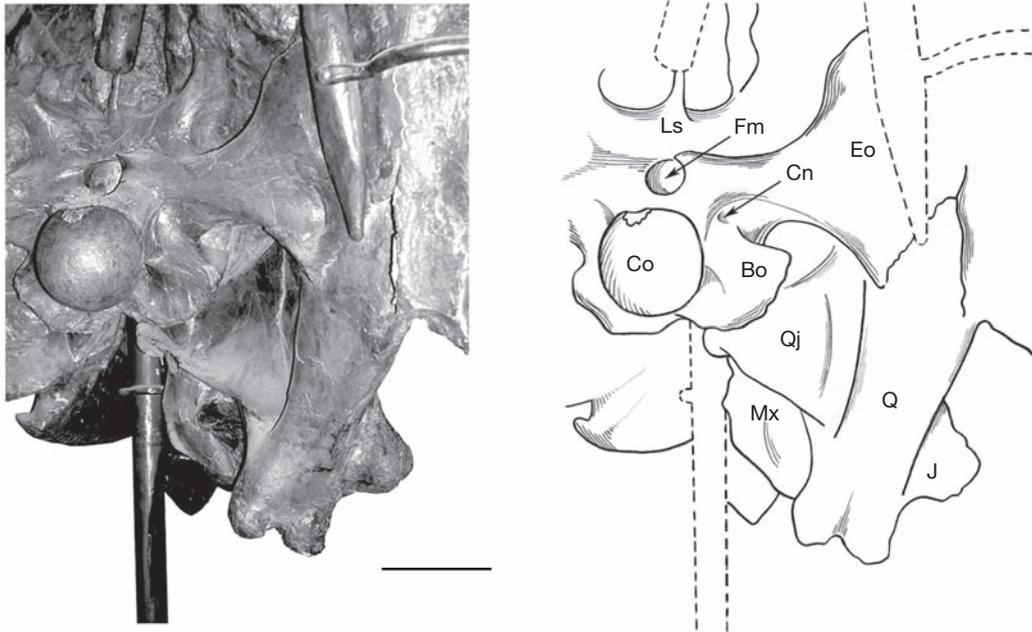


FIG. 5. — *Triceratops horridus* Marsh, 1889; Upper Cretaceous, Lance Creek, Converse County, Wyoming, USA; braincase and right quadrate in posterior view (MNHN 1912.20). Abbreviations: **Bo**, basioccipital; **Cn**, cranial nerve; **Co**, occipital condyle; **Eo**, exoccipital; **Fm**, foramen magnum; **J**, jugal; **Ls**, laterosphenoid; **Mx**, maxilla; **Q**, quadrate; **Qj**, quadratojugal. Scale bar: 10 cm.

that it probably played a role in the protection of the eyes. An interesting feature is visible on this skull roof at the caudal limit of the frontals and at the base of the two massive brow horns: the presence of an open and cylindrical fontanelle, an indication of the incomplete growth of the specimen.

Postorbital (Po)

The postorbital is mainly represented by the brow horns, which are massive, slightly compressed laterally, and markedly curved. Brow horns are projected forward at an angle of approximately 50° relative to the ventral margin of the maxilla and display well marked vascular grooves. These indicate the possible presence of a horny sheath that entirely covered these horns in life (Forster 1996a). The suture between postorbital, squamosal and jugal can only be observed on the left side of skull.

Jugal (J)

The jugal forms a large process overhanging the internal part of the maxilla, like a lateral shield pro-

tecting the articular of the mandible and covering the quadrate and quadratojugal. Caudally, it forms the cranial and dorsal edge of the lower temporal fenestra, conformation discussed hereafter.

Quadrate (Q)

The quadrate projects behind the braincase beneath the frill. In lateral view, each quadrate is covered by the ventral process of the jugal and is separated from the latter by the quadratojugal. In caudal view, the quadrate appears vertical and thickens ventrally to form a robust articular condyle (visible only on the right side of skull).

Frill

The parietal (P), which displays a concave profile laterally, constitutes the central third of the frill, whereas its remaining two thirds are formed on both sides by the squamosals. At the level of the postfrontal fontanelle, at the most cranial limit of the parietal, there are two depressions behind the base of the brow horns, which probably

indicate the position of the supratemporal fenestra, covered by coating in the restoration. Also, the parietal was retouched at the time of the restoration. All of its caudal part, bordering the left squamosal, seems entirely reconstructed. The squamosal (Sq) has a convex dorsal margin caudally, and passes rostrally above the quadra-tojugal to outline the lower temporal fenestra, at the level of its ventral and caudal margins. At the margin of the squamosal, the sutured epoccipitals (E) are short, obtuse, partly fused together, and seem to become longer near the top of the frill. Lastly, the surface of the frill seems abundantly and finely vascularized even if accentuated by the restoration.

Braincase

The braincase is located under the frill, beneath the parietal. Many elements can be observed (Fig. 5): 1) The median occipital condyle (Co) is spherical (diameter of 9.7 cm) and ventrally projected. It confers a high degree of mobility to the skull, while its orientation suggests a tilted position of the head (Ostrom & Wellnhofer 1986). The foramen magnum located above the occipital condyle has a diameter of 3.7 cm.

2) The exoccipitals (Eo) form the lateral two thirds of the braincase, and form two large lateral expansions on both sides of the condyle. They support the squamosal at the upper end of the quadrate. The expansive development of these bones may be related to supporting the weight of the skull.

3) The basioccipital (Bo) represents the median third of the braincase and is located directly below the condyle. On each side of the condyle one can observe two pairs of foramina for the exit of cranial nerves IX to XII (Cn).

Predeontary

The edentulous predeontary is the only element of the mandible preserved for this specimen. Its dorsal margins are hollowed by a long groove. With traces of vascularization on its external surface, this groove seems to indicate the presence of a pointed horny beak that formerly covered the bone (Ostrom & Wellnhofer 1986).

ON THE SYSTEMATICS OF *TRICERATOPS*

Since the erection of the genus *Triceratops* by Marsh (1889), up to 16 species were assigned to it by various authors, on the basis of more or less complete material (Marsh 1889, 1890, 1891, 1898; Hatcher 1905; Hatcher *et al.* 1907; Lull 1915, 1933; Brown 1933; Schlaikjer 1935; Sternberg 1949). But more recently, only one (*Triceratops horridus* Marsh, 1889) or two species (*T. horridus* and *T. prorsus* Marsh, 1890) are considered within the genus (Dodson 1996; Dodson *et al.* 2004).

The hypothesis of a small number of species appears indeed the most acceptable intuitively, because one or two species of *Triceratops* is more reasonable with what is known of the biology of large living tetrapods. Indeed, up to 16 contemporaneous species of *Triceratops* in an area the size of Wyoming would be comparable to the same number of living species of elephants and rhinoceroses, represented only by one and two species, respectively, in present-day Africa (Ostrom & Wellnhofer 1986). There are in fact many ecological reasons that such a large number of species of large animals do not inhabit the same region, notably the competition for food resources.

Although alluded by Ostrom & Wellnhofer (1986) in their interpretation of the intraspecific variability, the concept of sexual dimorphism in *Triceratops* was first proposed by Lehman (1990). Indeed, it seems reasonable to consider that such large animals can also display sexual dimorphism, their horns and frill being potential secondary sexual characters. However, it is interesting to note that opinions differ on this question. Forster (1996b) argued that this monospecific interpretation with sexual dimorphism would imply that the females are more abundant than the males in palaeontological records. In contrast, Dodson (1996) argued that this ratio sounds reasonable from a biological point of view, always based on living examples: in elephants and zebras, for example, the males have a mode of life which is more dispersed and solitary. Thus, according to Dodson (1996), the hypothesis of sexual dimorphism, although not obvious from the fossil record, has to be considered in more detail. However, Goodwin *et al.* (2006), after the description of the smallest known

Triceratops skull of a juvenile individual, conclude that cranial ornaments in ceratopsids (horn and frill appearance) represent more probably visual organs for species communication rather than for sexual display or agonistic encounters, because they appear at an early ontogenetic stage.

Lastly, Forster (1996b) proposes some characters to discriminate two species within the genus *Triceratops* (rostral shape, horns length notably). But Lehman (1998) considers these species as two extreme morphotypes in a morphological cline (Lehman 1998). Moreover, it is interesting to note that the Paris specimen MNHN 1912.20 presents some intermediate features:

– first, in the majority of the specimens studied by Forster (1996b), the jugal forms the dorsal rim of the lower temporal fenestra (referred to *Triceratops horridus*), whereas in some specimens this rim is formed by the squamosal (referred to *Triceratops prorsus*). But the Paris specimen presents an intermediate sutural configuration, both the jugal and the squamosal bound dorsally the lower temporal fenestra (Fig. 3);

– second, the nasal horn presents a great variety of forms and sizes and has often been considered as a specific character. Forster (1996b) defined thus two states: a short and erect horn (referred to *Triceratops horridus*) or a long, curved and forward-directed horn (referred to *Triceratops prorsus*). However MNHN 1912.20 displays the combination of a reduced size and very marked forward slant.

It is also interesting to note that the other characters proposed by Forster (brow horn length or rostral shape) display in fact much variability, as suggested by Lehman (1990, 1998). It is worth noting that these characters are traditionally the most frequently cited features to define the various *Triceratops* species.

Moreover, Lehman (1998) shows that there is no geographic or stratigraphic separation between the two species proposed by Forster, whereas no extant genus of large tetrapods (elephant, hippopotamus, rhinoceros) presents sympatric species.

Therefore, according to the Ostrom & Wellnhofer (1986) and Lehman (1990, 1998) conception, considering only one *Triceratops* species, the Paris specimen is here referred to *Triceratops horridus*.

CONCLUSION

The *Triceratops* skull curated in the gallery of palaeontology of Muséum national d'Histoire naturelle of Paris is a best preserved specimen, whose frill restoration is however debatable. Although previously ignored, this specimen should be considered in the debate about the taxonomy of *Triceratops* because of its intermediate morphology within the *Triceratops* morphocline. In agreement with the currently accepted monospecific model implying high variability, the specimen MNHN 1912.20 previously referred to *Triceratops calicornis* is here re-assigned to *Triceratops horridus*.

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