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3D external restorations of stegocephalian skulls using *ZBrush*: The *renaissance* of fossil amphibians

Reconstitutions externes 3D de crânes de stégocéphales sous ZBrush : la renaissance des amphibiens fossiles

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ABSTRACT

Cranial soft tissues (eyes, dermis, muscles, etc.) have never been preserved in fossil stegocephalians, and few specific studies have been done on their related osteological features (such as dermosensory canals, dermal bone ornamentation and microstructure). Consequently, the most useful tool to reconstruct stegocephalians remains the actualistic comparison with analogous living ecomorphotypes. Coupled with numerical sculpturing technologies available with the software *ZBrush*, it is now possible to appreciate the cranial soft tissues in 3D and to better reconstruct the external skull structures. Examples are given of the early tetrapod *Acanthostega gunnari* from the Devonian of Greenland and the Triassic temnospondyls *Edingerella madagascariensis* from Madagascar and *Parotosuchus* sp. from Antarctica. This palaeontological application of *ZBrush* is one of its first scientific uses. The obtained reconstructions are useful for scientific publication and in return they allow palaeontologists to better understand the palaeobiology of extinct organisms.

RÉSUMÉ

Les tissus mous du crâne (yeux, derme, muscles, etc.) n'ont malheureusement jamais été préservés chez les stégocéphales (ou amphibiens fossiles au sens large). Cela rend leur reconstitution *in vivo* très difficile. Les caractères crâniens associés à des tissus mous sont, entre autres, les canaux sensoriels dermiques (qui courent en surface ou à l'intérieur des os dermiques), l'ornementation et la structure histologique de ces os, la boîte crânienne, les foramens nutritifs ou nerveux et les crêtes osseuses ou apophyses musculaires. Peu d'études spécifiques ont été réalisées sur ces caractères. Par conséquent, l'outil le plus adapté pour reconstruire ces amphibiens fossiles demeure la comparaison actualiste avec des écomorphotypes analogues et vivants. Couplée avec les technologies de sculpture

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numérique disponibles grâce au logiciel *ZBrush*, il est désormais possible d'apprécier les tissus mous du crâne en 3D et de mieux reconstruire les structures crâniennes externes des tétrapodes anciens. Des exemples sont donnés ici avec trois taxons : *Acanthostega gunnari*, un des premiers tétrapodes, du Dévonien du Groenland, et les temnospondyles triassiques *Edingerella madagascariensis* de Madagascar et *Parotosuchus* sp. d'Antarctique. Cette application paléontologique de *ZBrush* correspond à une des premières utilisations scientifiques du logiciel. Les reconstitutions *in vivo* obtenues, hyper-réalistes, sont très utiles pour la diffusion des sciences, et permettent en retour de mieux comprendre la paléobiologie de ces organismes éteints.

1. Introduction

The oldest tetrapods (as body-fossils or skeletal remains) are dated from the Late Devonian (e.g., Clack, 2002, 2006a; Coates et al., 2008), but their evolutionary history began earlier (e.g., Steyer, 2009), during the Middle Devonian based on recently discovered footprints (Niedźwiedzki et al., 2010). The first tetrapods were non-amniotes ("amphibians" *sensu lato*), polydactylous, and they are considered here as "stegocephalians" (a non-homogeneous group of fossil amphibians). The stegocephalians are linked with the living tetrapods (i.e., amniotes and lissamphibians), but the origins of the latter are still highly debated (see e.g., Anderson, 2008; Laurin, 1998; Ruta et al., 2003 for hypotheses on lissamphibian origin(s)).

The stegocephalians presented a very wide spectrum of external morphologies (e.g., crocodiloid, gavialoid, salamandroid) and adult sizes (several centimeters to 7 m. total body length, e.g., Steyer and Damiani, 2005). Preservation of soft tissues is extremely rare in stegocephalians: few cases of skin impressions or muscular tissues have been reported, for example, in small branchiosaur temnospondyls (Heyler, 1994) or in aistopod lepospondyls (Germain, 2008) from Montceau-les-Mines, a famous Carboniferous-Permian Lagerstätte in France. These dermal or muscular remains help us to better understand the life history traits, biomechanics and palaeobiology of these extinct taxa. However, for the cranial features, unfortunately no soft tissues (eye, tongue, skin, etc.) have been discovered so far. Consequently, it is still very difficult to propose detailed living reconstructions of the whole organisms.

This article describes a new, preliminary 3D analysis restoring stegocephalian taxa based on (1) actualistic comparisons with living analogous ecomorphotypes, and (2) new 3D sculpturing and modelling methodologies using the powerful *ZBrush* software. These newly proposed restorations allow us: (1) to test the actualistic model chosen in the comparisons; and (2) to better understand the palaeobiology of these enigmatic fossil organisms.

2. Material

Institutional Abbreviations – MNHN, Muséum national d'Histoire naturelle, Paris, France; MSNM, Museo di Storia Naturale di Milano, Italy; UWBM, Burke Museum of Natural History and Culture, Seattle, USA.

Three different stegocephalian taxa have been chosen for this analysis based on their different circumstances of preservation, and their geographic and geologic origins. The aim of this study is to test the quality of the software used here, and to see whether this 3D methodology is useful (Figs. 1–3).

The taxa reconstructed here are:

Acanthostega gunnari (Jarvik, 1952), an early tetrapodomorph from the Upper Devonian of Greenland. Its reconstruction is mostly based on morphological data and 2D illustrations from the literature (e.g., Clack, 1994; Clack, 2000) including the 3D skeletal reconstruction (or "model") of Goldfinger (1997, in Clack, 2006b), the reconstruction of the skull in lateral view (Clack, 1997), and the reconstructions of the whole skeleton in lateral view (Ahlberg et al., 2005; Murphy, 2005) (Fig. 1).

Edingerella madagascariensis Lehman, 1961 (Maganuco et al., 2009; Schoch and Milner, 2000) a capitosaurian temnospondyl (*sensu* Schoch and Milner, 2000 = mastodonsaurian *sensu* Damiani, 2001) from the Lower Triassic of Madagascar (Fig. 2). Its cranial reconstruction is based on direct examination of specimens MNHN MAE3000a/b, MNHN MAE3002a/b, MNHN MAE3003a/b/c (holotype), MNHN MAE3004, MNHN MAE3005a/b, MNHN RHMA02, MSNM V2992, MSNM V3880, and MSNM V6237 (see also Maganuco et al., 2009). This species is known from various and well preserved skulls ranging from the juvenile to the adult stage (Steyer, 2003). The anterior portion of the postcranial region of *E. madagascariensis* is also restored based on the postcranial material (pectoral girdle, left humerus, and disarticulated anterior vertebrae and ribs) preserved in MNHN MAE3002a/b, MNHN MAE3003a/b/c, MNHN MAE3032, MNHN RHMA02, and MSNM V6237.

Parotosuchus sp., a capitosaurian temnospondyl from the Middle-Late Triassic of Antarctica (Fig. 3). Its cranial reconstruction is based on direct examination of the specimen UWBM 88571 (cast deposited in the MNHN), a right portion of the rostrum preserving the external naris and choana in articulation with the anterior portion of the corresponding mandible (Sidor et al., 2007; Steyer et al., 2007).

3. Method

As the methodology deals with numerical 3D sculpturing (which is not infography *sensu stricto*), the software used here is *ZBrush* version *3.5 R3*, a powerful 3D modelling tool often used by "Creature Designers" (a specific

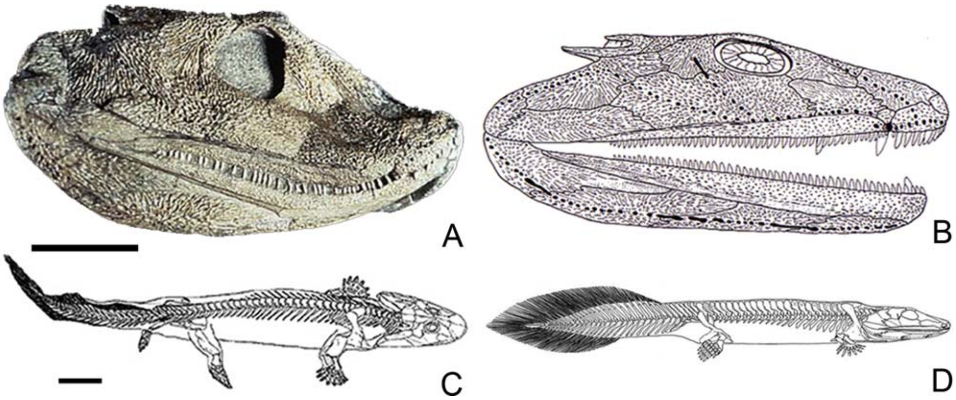

Fig. 1. Material of *Acanthostega gunnari* (Late Devonian of Greenland) used in the analysis; Photo (**A**) and reconstruction of the skull (**B**) (Clack, 2000), scale bar 5 cm; reconstructions of the skeleton in lateral view (**C**, from Clack, 2006b; **D**, from Ahlberg et al., 2005), scale bar 10 cm.

Fig. 1. Matériel relatif à *Acanthostega gunnari* (Dévonien supérieur du Groenland) utilisé dans l'analyse ; Photo (**A**) et reconstitution (**B**) du crâne (Clack, 2000), échelle 5 cm ; reconstitution du squelette en vue latérale (**C**, d'après Clack, 2006b ; **D**, d'après Ahlberg et al., 2005), barre d'échelle 10 cm.

term which gathers biologists and anatomists working for the cinema, i.e., imagining more or less viable bestiaries for Science-Fiction and/or Fantasy movies). This palaeontological application of *ZBrush* is therefore one of the first scientific use of the software. We will not describe the specific use of *ZBrush*, as it is already available in the software tutorial (www.zbrushcentral.com).

The palaeontological application of *ZBrush* proposed here includes three main steps, from fossil observation to the living (or *in vivo*) reconstruction.

Step 1 (the skull in 3D): a 3D version of the skull is sculpted under *ZBrush*, based on the (2D) anatomical plate describing it (Fig. 3B). The more views that are available on the anatomical plate (dorsal, palatal, occipital, lateral, etc.), the more reliable is the sculpture. This step is made by the sculptor/modellor (MB) and validated by the palaeontologist (JSS). This step could be replaced by a scan of the skull (tomographic or surface scan) and its importation under *ZBrush*.

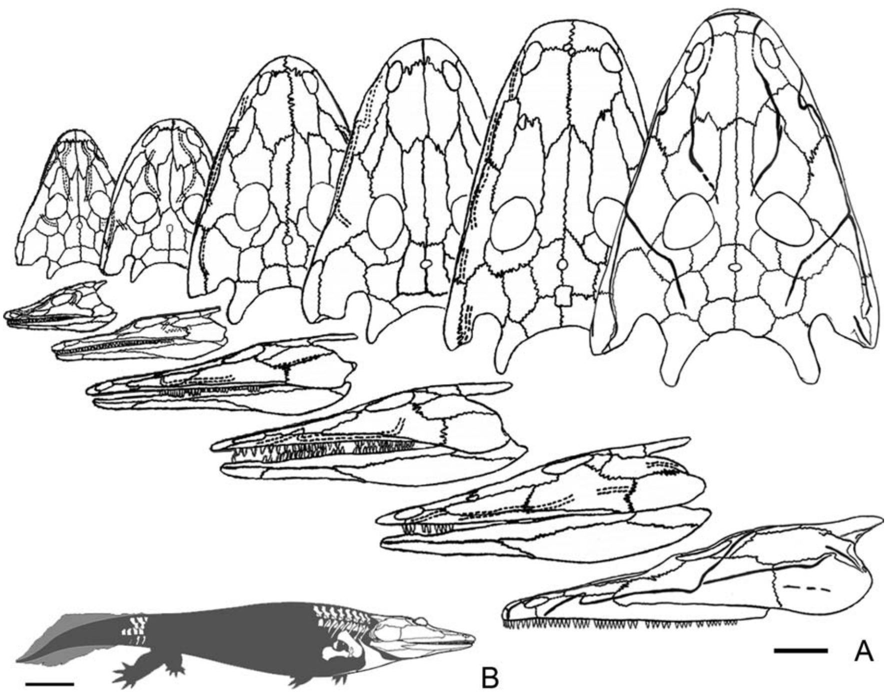

Fig. 2. Material of *Edingerella madagascariensis* (Early Triassic of Madagascar) used in the analysis; **A**, cranial growth series from the juvenile to the adult individual (from Maganuco et al., 2009; Steyer, 2003), scale bar 2 cm; **B**, reconstruction of the adult skeleton in lateral view (Maganuco et al., 2009), scale bar 7 cm.

Fig. 2. Matériel relatif à *Edingerella madagascariensis* (Trias inférieur de Madagascar) utilisé dans l'analyse ; **A**, série de croissance crânienne, de l'individu juvénile à l'adulte (d'après Maganuco et al., 2009 ; Steyer, 2003), échelle 2 cm ; **B**, reconstitution du squelette adulte en vue latérale (Maganuco et al., 2009), barre d'échelle 7 cm.

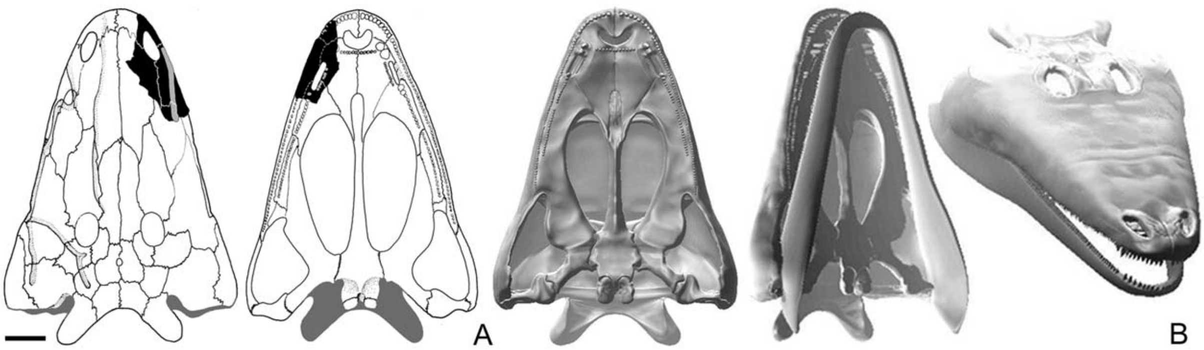

Fig. 3. Material of *Parotosuchus* sp. (Middle-Late Triassic of Antarctica) used in the analysis; **A**, reconstruction of the skull in dorsal and ventral views based on *Parotosuchus orenburgensis* (from Schoch and Milner, 2000; Sidor et al., 2007), preserved region of the skull in black; **B**, 3D model of the skull made with *ZBrush*. Scale bar 10 cm.

Fig. 3. Matériel relatif à *Parotosuchus* sp. (Trias moyen-supérieur d'Antarctique) utilisé dans l'analyse ; **A**, reconstitution du crâne en vues dorsale et ventrale, basée sur *Parotosuchus orenburgensis* (d'après Schoch and Milner, 2000 ; Sidor et al., 2007), avec région du crâne préservée en noir ; **B**, modèle 3D du crâne effectué sous *ZBrush*. Barre d'échelle 10 cm.

Step 2 ("dressing" the skull): this corresponds to the reverse methodology than that used during a dissection (Fig. 4): the skull is "covered" by virtual soft tissues deduced from the morphology of the bones. Layer by layer, the eyeballs are reconstructed based on the shape and size of the orbits, the tongue is positioned in the mouth, and so on up to the restoration of the cranial muscles (palaeomyology). This process is scientifically based on the development of the bony crests or apophyses, the bone proportions, the pattern of the jaw articulation, and so on. This step, the longest and the most important one, is the result of a close and multidisciplinary collaboration between the palaeontologist and the sculptor (Moltenbrey, 2008). This collaboration allows in return the palaeontologist to test the validity of the original anatomical figures and potentially to raise new questions about life history traits of the taxa restored. For example, the restoration of the cranial muscles at the level of the neck and the jaw help to investigate the range of the possible movements of the head along the body, of the mouth, of the strength of the bite, etc.

Step 3 (the final touch): the last virtual layer corresponds to the dermis covering the head and the neck. This dermal reconstruction is directly mapped on the 3D model. For the skull roof, the skin texture is reconstructed based on the ornamentation of the dermal bones and their inner microstructures, when available (e.g., Witzman,

Fig. 4. Reverse virtual dissection under *ZBrush*. The skull is reconstructed by successive 3D layers of soft tissues covering step by step the bones. Examplified here with the skull of the Asiatic wild pig (*Babyrousa babyrussa*).

Fig. 4. Dissection virtuelle inversée sous *ZBrush*. Le crâne est reconstruit par couches 3D successives de tissus mous couvrant étape par étape les différentes parties du crâne. Exemple de reconstitution crânienne à partir du crâne du cochon sauvage asiatique (*Babyrousa babyrussa*).

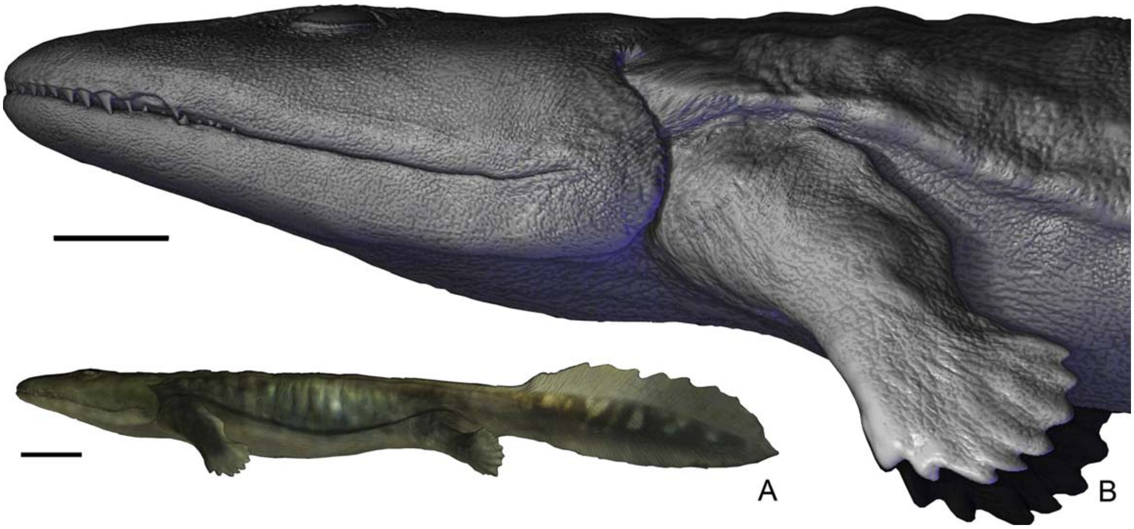

Fig. 5. 3D Reconstruction of *Acanthostega gunnari*, early tetrapod from the Upper Devonian of Greenland. **A**, whole body, scale bar 5 cm; **B**, details of the head and anterior part of the postcranial region, scale bar 2 cm; both in laterial view.

Fig. 5. Reconstitution 3D de *Acanthostega gunnari*, un des premiers tétrapodes, Dévonien supérieur du Groenland. **A**, corps entier, échelle 5 cm; **B**, détails de la tête et région antérieure du corps; en vue latérale, barre d'échelle 2 cm.

2009). Extant taxa with similar skull roof ornamentation and texture are sought out and the corresponding dermis is observed. The overlying skin does not always directly follow the underlying features in extant taxa, from the fish *Amia* to the frog *Ceratophrys cornuta*. Except for exceptional cases (preservation of skin impression or colour pattern, e.g., Werneburg, 2007), the colour of the skin is interpreted based on actualistic comparisons of analogous ecomorphotypes. This final step is made by the texturer (SL) who proposed to the team a set of several possible dermal samples.

The advantage of this proposed method is that *ZBrush* allows us to reconstruct the extinct organism layer by layer, directly in three dimensions, and to any given scale. After the texture layer (step 3), the result is hyperrealistic.

4. Results and discussion (Figs. 5–7)

4.1. *Acanthostega gunnari*

A preliminary 3D reconstruction of the whole organism is proposed (Fig. 5A), based on two reconstructions of the whole skeleton from the literature (Clack, 2006b; Murphy, 2005; see also section "Material"). It shows peculiar morphological and adaptive features such as a relatively elongated and (dorsoventrally) flat body, except for the high tail and its protocercal fin. This caudal fin is reconstructed based on the elongate and almost symmetrical dorsal and ventral finrays, as well as their well-developed internal supports (supra and infra-neural spines) (Coates, 1996).

Particular attention has been paid to the anterior part of the body, from the tip of the snout to the thoracic region (Fig. 5B): this more detailed reconstruction shows a relatively flat and triangular head with small, marginal external nostrils placed close to the jaw margin (Clack, 1994). The eyeballs, dorsally oriented, are considered as very globular based on the sclerotic rings preserved inside the orbits (Clack, 1997). Gills are not reconstructed here, because they were probably internal (Clack, 2000; Lebedev and Coates, 1995). This cranial complex is followed by a short neck (based on the relatively short atlas-axis complex) as well as short and polydactylous forelimbs. This reconstruction also presents well developed interdigital skin between the long anterior digits. Although not preserved on the fossil specimens, these presumably soft interdigital skins are hypothesized based on 1) the pattern of the autopodium (size, shape of the phalanges, and their connection with the metacarpals) and 2) biomechanical discussions (extracted from the literature) dealing with primarily function(s) of these paddle-like forelimbs (e.g., Coates, 1991; Coates, 1996). The ornamentation of the skull roof bones, as preserved, suggests a bumpy but relatively thin skin texture similar to the leathery integuments observed in living crocodilians (JSS, pers. obs.), whereas the neck and the thoracic-abdominal complex of *Acanthostega* is a priori covered by smoother skin and by small elongate ovoid scutes ventrally (Coates, 1996; Coates and Clack, 1995).

4.2. *Edingerella madagascariensis*

Interestingly, this species was euryhaline and probably lived in brackish or shallow marine waters based on its associated fauna (Maganuco et al., 2009; Yanbin et al., 2002). Moreover, both preserved juvenile and adult individuals (see Material section) suggest a relatively rapid allometric growth, probably more similar to that of reptiles than that of lissamphibians (Steyer, 2003). These observa-

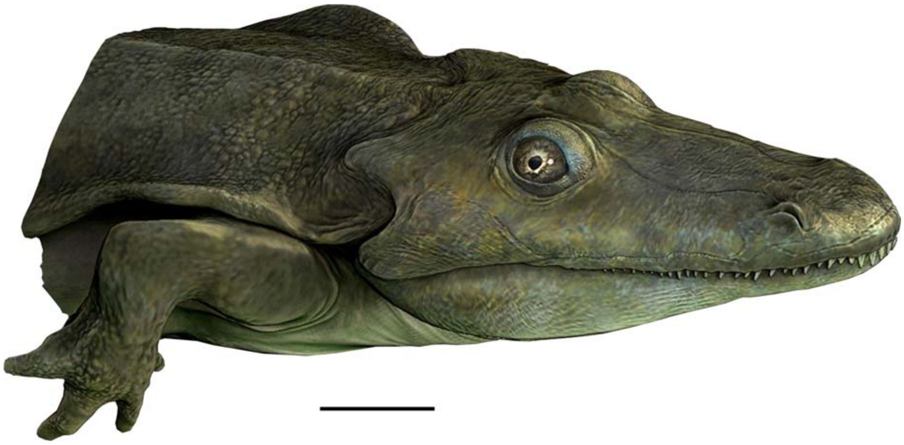

Fig. 6. 3D Reconstruction of *Edingerella madagascariensis*, capitosaurian temnospondyl from the Early Triassic of Madagascar, scale bar 3 cm.
Fig. 6. Reconstitution 3D de *Edingerella madagascariensis*, temnospondyle capitosaure du Trias inférieur de Madagascar, barre d'échelle 3 cm.

tions, together with its skeletal proportions, suggest that the ecomorphotype of *E. madagascariensis* might be analogous between the marine crocodile (*Crocodylus porosus*) and the marine iguana (*Amblyrhynchus cristatus*). These two living species could therefore be useful to reconstruct the external body shape of *E. madagascariensis* (Fig. 6).

The *ZBrush* reconstruction of *E. madagascariensis* exhibits a triangular and longirostral head (Warren and Hutchinson, 1988), with large and dorsolaterally oriented eyeballs. We prefer to reconstruct a globular eyeball and a circular pupil, rather than a slit pupil (vertical or horizontal) because this character (slit pupil) presents a larger variability among tetrapods (Malmström and Kröger, 2006). We refer to Maganuco et al., 2009 (p. 45–46) for the reconstruction of the cranial myology. Taking into account the aquatic way of life and hunting strategy of *Edingerella* (e.g., Maganuco et al., 2009; Steyer, 2003), we also inferred slightly elevated "blowholes" covering the external nostrils. Such nasal dermal integuments would allow the animal a sub-horizontal position at the water surface in order to observe and to breathe at the same time (as is the case, again, in living crocodiles). Similar soft nasal tissues have also been inferred in the crocodiloid *Nigerpeton ricqlesi*, a Permian cochleosaur temnospondyl from Niger (Steyer et al., 2006). At least, the dermis of *Edingerella* was presumably tightly attached to the skull roof bones, rendering their ornamentation externally visible to some degree (Maganuco et al., 2009), as is the case in living crocodiles.

4.3. *Parotosuchus sp.*

The 3D restoration of *Parotosuchus* proposed here is based on very fragmentary material (UWBM 88571 from Antarctica, Sidor et al., 2007; see above) (Fig. 7). The missing cranial bones have been reconstructed according to Bryant and Russell (1992) who proposed to restore the unpreserved characters using those of the closest related taxa. The species *Parotosuchus orenburgensis* (Schoch and Milner, 2000) is therefore used to complete the skull (Fig. 7A). The obtained restoration is testing, in return, the efficiency

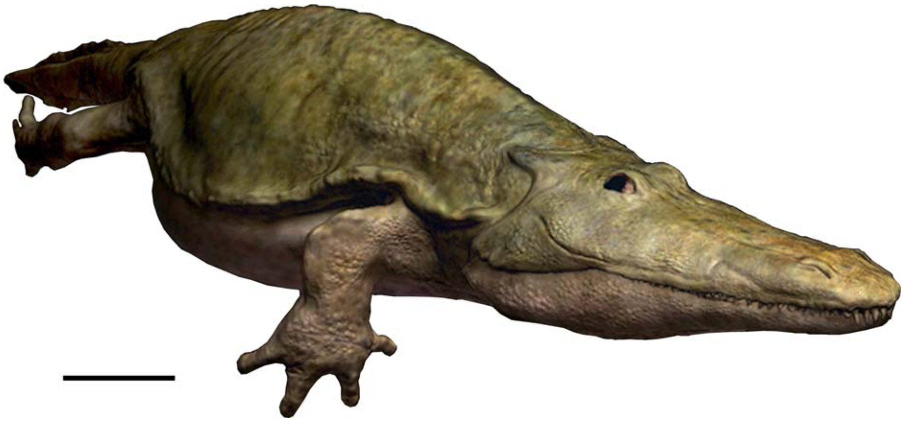

Fig. 7. 3D Reconstruction of *Parotosuchus* sp., capitosaurian temnospondyl from the Middle-Late Triassic of Antarctica, scale bar 20 cm.
Fig. 7. Reconstitution 3D de *Parotosuchus* sp., temnospondyle capitosaure du Trias moyen-supérieur d'Antarctique, barre d'échelle 20 cm.

of the software *ZBrush* in this case of very fragmentary material. This obtained restoration of *Parotosuchus* from Antarctica (Fig. 7B–C) shows a very longirostral but relatively high head, partly connected to the body by robust and high tabular horns. The dorsal eyeballs are small relative to the snout, and the external nostrils slightly projected vertically. The dermosensory canals are still visible. UWBM 88571 shows a very dense and sculptured ornamentation largely consisting of a honeycombed pattern (Sidor et al., 2007). Interestingly, the labial region of the premaxilla, maxilla, and dentary is less ornamented along the tooth row than on the skull roof or on the mandible (Maganuco et al., 2009). This relatively smooth outer surface of the bones surrounding the mouth has been interpreted as supporting lips, useful soft tissues which allow an hermetic closure of the mouth underwater (Janvier, 1992). *Parotosuchus* is restored with its teeth visible (Fig. 7) because we hypothesize retractable lips.

The postcranial region of *Parotosuchus* has also been preliminarily restored following the methodology of Bryant and Russell (1992): the body proportions of *Mastodonsaurus giganteus* (Schoch, 1999), the closest taxon with the best-known postcranial skeleton, were applied to our model. The skin infoldings separating the dorsal surface from the ventral one are extrapolated based on the dermo-lateral adipose tissues observed in *Andrias japonicus*. They have been added by the sculptor (MB) to render the restoration more hyperrealistic.

5. Conclusion

ZBrush is a very powerful tool for 3D palaeontological external reconstructions. The 3D cranial sculptures presented here correspond to one of the first scientific uses of the software, and are the result of a long and close multidisciplinary cooperation between a senior organic modeller (MB, also *ZBrush* Beta Tester), a texturer (SL) and a palaeontologist (JSS) (Moltenbrey, 2008). These 3D restorations are useful for transmission of science to the public, and in return they also allow palaeontologists to better understand the palaeobiology of extinct organisms.

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Web links: We invite the readers to follow the 3D *renaissance* of the early tetrapods (and others) at: www.hox.fr, www.marcboulay.net, www.sylvialorrain.net.

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