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Revision of the crocodylians from the Oligocene of Monteviale (NE Italy) and the diversity of
European eusuchians across the Eocene-Oligocene boundary

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RH: MACALUSO *ET AL.*—OLIGOCENE CROCODYLIANS FROM MONTEVIALE

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ABSTRACT—Crocodilian remains from the Oligocene fossil locality of Monteviale, northeastern Italy, have historically been referred to different genera, but all material was recently assigned to *Diplocynodon* cf. *D. ratelii* Pomel, 1847. The purpose of the present work is to clarify the systematics of the known crocodilian remains from Monteviale. The largest collection is housed in Padua (Italy), but museums in La Rochelle (France), Basel (Switzerland) and London (UK) host crocodilian remains whose uncertain provenance is either Monte Bolca or Monteviale. Radiogenic strontium isotope ratios were measured on the embedding lignite of those specimens to investigate their provenance. The material belongs to the genus *Diplocynodon*, but it clearly differs from *D. ratelii* because the nasal elements are excluded from the external nares. *Diplocynodon* from Monteviale shares the same general suture pattern of the skull with the two species *D. tormis* and *D. muelleri*. *Diplocynodon muelleri* and specimens from Monteviale are also congruent in terms of shape and proportion of the supratemporal fenestrae. However, a revision of *D. muelleri* is currently needed, thus the Monteviale species is identified as *Diplocynodon* cf. *D. muelleri*. In order to examine the relationships of *Diplocynodon* from Monteviale, a phylogenetic analysis was carried out, which does not point to particularly close relationship among *D. muelleri*, *D. tormis*, and the *Diplocynodon* from Monteviale. The occurrence of *Asiatosuchus* in Monteviale is discarded, supporting the hypothesis of a reduction in crocodilian diversity around the Eocene-Oligocene boundary in Europe.

INTRODUCTION

It has been suggested that the composition of the freshwater crocodilian fauna of Europe may have been affected by climatic deterioration around the Eocene-Oligocene boundary (33.9 million years ago; Markwick, 1998; Martin, 2010). Indeed, a marked decline

in diversity is observed between the greenhouse Eocene assemblages, when the European crocodylian fauna is comprised of at least four taxa per locality (with a maximum of seven taxa for Messel; Berg, 1966; Morlo et al., 2004; Hastings, 2017), and the subsequent cooler Oligocene assemblages, wherein each locality hosts the single genus *Diplocynodon*.

Diplocynodon is therefore thought to have survived dramatic climatic change (see Martin, 2010, for a review).

Italy possesses a rich Cenozoic record of crocodylians (Kotsakis et al., 2004; Delfino et al., 2007; Piras et al., 2007; Abbazzi et al., 2008; Delfino and Rook, 2008; Delfino and Rossi, 2013; Colombero et al., 2017). Among the most famous localities, the lignite deposits from the Eocene of Monte Bolca and the Oligocene of Monteviale have yielded many, often articulated, specimens. Crocodylians from Monte Bolca were attributed to two different taxa by Sacco (1895): *Crocodylus vicetinus* Liroy, 1865, and *Crocodylus bolcensis* Sacco, 1895. The taxonomic affinity of this material is unclear and awaits revision, but there are currently at least three taxa identified: *Asiatosuchus*, *Allognatosuchus* and *Boverisuchus* (Kotsakis et al., 2004). The reported presence of a species of *Diplocynodon* at Monte Bolca (Papazzoni et al., 2014) is erroneous, as the only specimen (MGP-PD 27403) of this genus labelled as coming from this locality is most likely from Monteviale (see below; Del Favero, 1999, Kotsakis et al., 2004). At the beginning of the 20th century, two species from the Oligocene locality of Monteviale were erected: *Crocodylus monsvialensis* Fabiani, 1914, and *Crocodylus dalpiazii* Fabiani, 1915. Fabiani (1914) remarked that *C. monsvialensis* had close affinities with *C. vicetinus* from Monte Bolca, but differed substantially enough to be designated as a new species. Fabiani (1914) briefly listed differences in shape and size of the temporal fenestrae, position of the frontoparietal suture, proportions of the frontal and prefrontal elements, and shape of the nares. Later, Berg (1966:40) proposed that *Diplocynodon* Pomel, 1847, was possibly present at Monte Bolca and Monteviale. He also proposed that some remains from

Monteviale shared the same characters with what he referred to as “*Crocodylus*” *vicetinus* from Monte Bolca, probably belonging to the same taxon.

The latest comprehensive revisions of the crocodylian assemblage from Monteviale date from the early 1990s. Two taxa were recognized: *Diplocynodon dalpiazii* (Fabiani, 1915) by Franco *et al.* (1992) and *Asiatosuchus monsvialensis* (Fabiani, 1914) by Franco and Piccoli (1993). However, both Rauhe and Rossmann (1995) and Kotsakis *et al.* (2004) expressed doubts about the presence of two species at Monteviale, suggesting that all these crocodylians belong to a single species of *Diplocynodon* instead. This view was also supported by Brinkmann and Rauhe (1998) in their description of a new specimen from the late Early Oligocene of Céreste, southern France, pertaining to the species *Diplocynodon ratelii* Pomel, 1847. Del Favero (1999) provided a detailed description of the problematic specimen then thought to be from Monte Bolca (MGP-PD 27403), which she referred to *Diplocynodon cf. ratelii*. Nannofossils in the matrix surrounding that specimen revealed that it was geologically younger, and therefore from Monteviale. Delfino and Smith (2009) mentioned that the youngest representatives of *Asiatosuchus* could be those from Monteviale if “the referral of ‘*Crocodylus*’ *monsvialensis* (Fabiani, 1914) to crocodyloids by Franco and Piccoli (1993) is valid. Finally, Pandolfi *et al.* (2016) provided a brief description of the crocodylians from Monteviale, attributing them to a single taxon, *Diplocynodon cf. ratelii*.

As shown above, the history of the knowledge of the Monteviale crocodylians is rather convoluted and the precise composition of the assemblage is somewhat still unclear. Although the systematic affinities of these crocodylians have been discussed by various authors, a detailed account of the osteology of the Monteviale crocodylians has yet to be carried out. The works of Franco *et al.* (1992) and Franco and Piccoli (1993) consist of an exhaustive catalogue of the specimens, but do not include full osteological descriptions based on

diagnostic characters. In this context, the presence of *Asiatosuchus* and *Diplocynodon* in the Oligocene of Monteviale remains to be verified.

We herein provide a detailed osteological description of the Monteviale specimens, housed in the collection of the “Museo Geologia e Paleontologia” of Padua, Italy, and of two previously unreported skeletons housed in the collections of the Musée de La Rochelle, France, and the Naturhistorisches Museum in Basel, Switzerland, that may come from the same locality. This description offers a basis to evaluate the presence of two sympatric taxa in the crocodylian assemblage of Monteviale. We intend to verify if the idea that the diversity of the Oligocene crocodylian assemblage of Italy is really an exception if compared to the European standard, or if the occurrence of *Asiatosuchus* should be discarded, thus confirming the hypothesis of a major reduction in the diversity of crocodylian assemblages around the Eocene-Oligocene boundary.

Ambiguous Provenance

The Monteviale origin of the specimens housed in Padua is well confirmed in the catalogues of the museum (except for MGP-PD 27403, most likely from Monteviale labelled as coming from Monte Bolca; see Del Favero, 1999, and Kotsakis et al., 2004). The provenance of the two previously unreported crocodylian skeletons is discussed below. They were donated to the collections of Basel and La Rochelle, where they are currently kept, at the beginning of the 20th century.

The Basel specimen does not bear any label and thus, the knowledge of its provenance is uncertain. The catalogue of entries at the Naturhistorisches Museum in Basel records in 1904 “Bc. 6. *Crocodylus* spec. Vorderer Theil eines Skeletes von oben sichtbar, mit gut erhaltenem Schädel” from the Lower Oligocene of Monte Bolca, this locality being also denoted as Monteviale (L. Costeur, pers. comm. to Jeremy Martin 2007). The crocodylian

skeleton of La Rochelle was purchased for 900 Francs from “Les Fils d’Emile Deyrolle”, a company based in Paris and providing natural history specimens for sale. The acquisition letter mentions a skeleton of *Crocodylus vicetinus* from Monte Bolca and is dated to the 10th of December 1931. The same specimen appears to be advertised in a natural history catalogue “Le Naturaliste” also published by “Les Fils d’Emile Deyrolle” and dated from 1908 (R. Vullo, pers. comm. to Jeremy Martin 2011).

The provenance and age of both specimens is therefore equivocal. The sites of Monte Bolca (middle Eocene) and Monteviale (early Oligocene) are located in the same Italian area, and Monte Bolca was, and still is, much more popular than Monteviale. Confusion about the provenance of fossils from these two localities has always been an issue, and Berg (1966) did not provide any extensive comment on this, just stating that the provenance of *Diplocynodon* from Monte Bolca or Monteviale was unclear. Kotsakis et al. (2004) and Pandolfi et al. (2016) reported that some mammals and crocodylians were likely to have been discovered at Monteviale and then referred by mistake to Monte Bolca. The catalogue of entries in Basel is consistent with such a possibility as the initial name of the locality (Monte Bolca) is crossed and replaced with “Monteviale”. Moreover, the collection is ordered stratigraphically and the crocodylian NMB-Bc.6 and associated mammal material from Monteviale are listed and placed in the upper Rupelian section (and thus among the Oligocene materials, not among the Eocene ones).

The designation of ‘Monte Bolca’ as a locality incorporates various fossiliferous sites of three different depositional environments: Monte Postale and Pesciara di Bolca consisting of micritic limestone deposited in a marine environment (Papazzoni et al., 2014); Spilecco consisting of marly limestones deposited in a shallow water environment (Papazzoni et al., 2014); Purga di Bolca and Vegroni consisting of lignite seams reminiscent of a freshwater depositional environment (Barbieri and Medizza, 1969; Del Favero, 1999). Only the Pesciara

di Bolca benefited from a recent detailed stratigraphic study and a middle Eocene age has been assigned to it (Papazzoni and Trevisani, 2006). An early-middle Eocene age has been proposed for Purga di Bolca (Papazzoni et al., 2014). That the museums of Basel and La Rochelle refer their specimens to Monte Bolca or to *Crocodylus vicetinus* (one of the species described on the basis of material from Monte Bolca) might be due to confusion with Monteviale, or these fossils could genuinely come from lignite sites of Purga di Bolca.

The two crocodylian skeletons from Basel and La Rochelle likely come from Monteviale on the basis of a morphological comparison and the similar encasing matrix of the material with the specimens housed in Padua, which certainly come from Monteviale. However, the assigning of provenance based on these factors is tentative. For this reason, a geochemical analysis comparing the matrix surrounding specimens of known and unknown provenance is presented below.

Institutional Abbreviations—**MLR**, Musée d’Histoire Naturelle de La Rochelle, France; **MGP-PD**, Museo di Geologia e Paleontologia dell’Università di Padova, Italy; **NHM-UK**, Natural History Museum of London, United Kingdom; **NMB**, Naturhistorisches Museum Basel, Switzerland.

MATERIAL AND METHODS

Material

The Monteviale material is subject to degradation connected to pyrite oxidation (see Larkin, 2011). To deal with this problem, during the past century the Padua material has been treated with several varnishes, which covered and obliterated most of the sutures among the bones, making the material very difficult to examine. The specimen housed in the

Naturhistorisches Museum in Basel is the best preserved, as it has been mechanically extracted from the slab and treated with ammonium gas and paraffin to preserve it from pyrite oxidation. The skeleton housed in La Rochelle remains within its original lignite matrix, unprepared in 3D. Most of the material is figured in Appendix 1.

Provenance Analysis

Lignites are sedimentary rocks formed from the aggregation of terrestrial plant material and thus they have a variable content of carbon. The plants that make up lignites grow on soil whose minerals originate from the weathering of substrates. Because geological substrates of different natures have their own radiogenic strontium isotope composition (expressed as $^{87}\text{Sr}/^{86}\text{Sr}$), so do soils that grow on it as well as associated plant remains and organisms that will feed on these plants, thus reflecting a local strontium isotope value (Graustein, 1989; Blum et al., 2000). The lignites of Purga di Bolca are several million years older (middle Eocene) than the lignites of Monteviale (early Oligocene) (Papazzoni and Trevisani, 2006; Papazzoni et al., 2014; Pandolfi et al., 2016) and should possess different geochemical compositions. Therefore, we predict that the radiogenic strontium isotope ratio (expressed as $^{87}\text{Sr}/^{86}\text{Sr}$) of samples from Purga di Bolca will differ from samples from Monteviale. To test this hypothesis, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were measured on two lignite samples from Purga di Bolca as well as on two specimens from Monteviale (MGP26855 and MGP26836). In addition, three samples of uncertain provenance including the two specimens presented above (La Rochelle and Basel), as well as one specimen housed in NHM-UK and labelled as coming from from Purga di Bolca, were analyzed. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were measured on a Nu instrument-500 multicollector-ICPMS with a Phoenix laser ablation inlet (Photon-Machines) at the Laboratoire de Géologie de Lyon. We are not aware of reference material for $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in lignite, so we used a homogenous standard of known strontium isotopic

composition (SRM-1400, Bone Ash) as a bracketing reference for correcting instrumental biases during measurements. The standard SRM-1400 contains 250 p.p.m. of strontium and produces about 3 volts on mass ^{88}Sr on the multicollector ICPMS. The standard SRM 1400 yields an average $^{87}\text{Sr}/^{86}\text{Sr}$ raw value of 0.71371 ± 0.00526 (2 s.d.), which is comparable to the TIMS value of 0.71310 ± 0.00002 (2 s.d.) (Schweissing and Grupe, 2003). Each sample was ablated three times with a spot diameter of 100 μm .

Phylogenetic Analysis

The Monteviale specimens were scored as a single taxon and included in the data matrix of Martin et al. (2014) for eusuchians, which contained a total of 97 taxa, 98 including the Monteviale crocodylian, and 179 characters (Appendix 2). The matrix was assembled using Mesquite (Maddison and Maddison, 2018). The characters are from Brochu et al. (2012; Appendix 3), which are the same used by Martin et al. (2014). All of the most informative species of *Diplocynodon* part of this data matrix: *Diplocynodon darwini*, *D. deponiae*, *D. hantoniensis*, *D. ratelii*, *D. muelleri*, *D. tormis*, and *D. remensis*. Another analysis was conducted that also included two less complete species of *Diplocynodon*, *D. elavericus* and *D. ungeri*, which were also included in some previous analyses (Martin, 2010; Martin and Gross, 2011; Martin et al., 2014). Replicates of 1000 random addition sequences were performed under TNT (Goloboff et al., 2003), using the traditional search with the TBR algorithm to search for shortest trees. *Bernissartia fagesii* was defined as the outgroup taxon as in Martin et al. (2014).

SYSTEMATIC PALEONTOLOGY

Order CROCODILIA Gmelin, 1789

Suborder EUSUCHIA Huxley, 1875

Superfamily ALLIGATOROIDEA Gray, 1844

Family DIPLOCYNODONTIDAE Hua, 2004

Genus DIPLOCYNODON Pomel, 1847

DIPLOCYNODON CF. *D. MUELLERI* (Kälin, 1936)

(Figs. 1–7)

Crocodylus monsvialensis Fabiani, 1914:233.

Crocodylus dalpiazii Fabiani, 1915:306.

“*Crocodylus*” *vicetinus* Liroy, 1865: Berg, 1966:58.

Diplocynodon dalpiazii (Fabiani, 1915): Franco et al., 1992:130, figs 2–17, pl. 1–3.

Asiatosuchus monsvialensis (Fabiani, 1914): Franco and Piccoli, 1993:101, figs. 3–12, pl. 1–3.

Asiatosuchus monsvialensis (Fabiani, 1914): Roccaforte et al., 1994:380.

Diplocynodon dalpiazii (Fabiani, 1915): Roccaforte et al., 1994:380.

Diplocynodon (Pomel, 1847): Rauhe and Rossmann, 1994: 84.

Diplocynodon ratelii Pomel, 1847: Brinkman and Rauhe, 1998:307–308.

Diplocynodon cf. *ratelii* Pomel, 1847: Del Favero, 1999:110.

Diplocynodon cf. *ratelii* Pomel, 1847: Pandolfi et al., 2016:13–14, figs. 9–10.

Referred material—See Appendix 1 for a complete description of all the specimens.

The material includes the two lectotypes: MGP-PD 26814 (lectotype of *Diplocynodon dalpiazii*) and MGP-PD 26843 (lectotype of *Asiatosuchus monsvialensis*). Besides them, the material housed in Padua includes: eight skulls (MGP-PD 10170, MGP-PD 11407, MGP-PD 28164, MGP-PD 26816 and MGP-PD 26817, (skull and lower jaw of the same individual), MGP-PD 26844, MGP-PD 26845, MGP-PD 26846, MGP-PD 26858); three rostri (MGP-PD

26815, MGP-PD 26850, MGP-PD 26862); nine isolated skull fragments (MGP-PD 8648, MGP-PD 26819, MGP-PD 26835, MGP-PD 26837, MGP-PD 26838, MGP-PD 26842, MGP-PD 26957, MGP-PD 26859, MGP-PD 31998); several disarticulated teeth (MGP-PD 26839); and various postcranial elements (MGP-PD 27999–26854 (a single, fractured slab), MGP-PD 26818, MGP-PD 26820, MGP-PD 26821, MGP-PD 26822, MGP-PD 26823, MGP-PD 26824, MGP-PD 26825 – 26830 (a single, fractured slab), MGP-PD 26826, MGP-PD 26827, MGP-PD 26828, MGP-PD 26829, MGP-PD 26831 - 26832 - 26833 - 26834 (derived from the same individual), MGP-PD 26836, MGP-PD 26840, MGP-PD 26841, MGP-PD 26847, MGP-PD 26848, MGP-PD 26849, MGP-PD 26851, MGP-PD 26852–26853 (a single, fractured slab), MGP-PD 26855, MGP-PD 26856, MGP-PD 31997). Besides the numbered specimens, in the Padua museum there are several specimens without numbers: seven fragments of mandibles and maxillae, more than 40 disarticulated teeth, five slabs with poorly preserved portions of the vertebral column, five isolated vertebrae, seven slabs with fragmentary and disarticulated limbs, and several ribs and osteoderms.

MGP-PD 27403 is the previously mentioned slab labelled "Monte Bolca," but as shown below via provenance analysis, it most likely comes from Monteviale. It contains an almost complete specimen which was described by Del Favero (1999).

NMB-Bc.6 is the anterior half of a skeleton with a complete skull showing its dorsal and ventral surfaces (Fig. 1); this slab also contains two areas (indicated with A and B in Fig. 1), with bones belonging to one or two smaller individuals.

MLR-no number, slab with a skeleton bearing a skull visible in dorsal view and disarticulated and fragmented portion of the postcranial skeleton.

NHM-UK 2789 is slab particularly altered by pyrite oxidation containing the thoracic portion of a small individual and part of its limbs.

Occurrence—Early Oligocene (late Rupelian) of Monteviale, Vicenza, north-eastern Italy (Pandolfi et al., 2016).

Description—Although most of the skulls are generally complete or only partially incomplete, the deformation is so intense that it is not possible to evaluate all those characters needed to establish the degree of inclination or orientation of structures (e.g. the direction of the internal choana or the orientation of the basioccipital under the occipital condyle).

Seven of the ten skulls housed in Padua preserve the lower jaw compressed against the maxilla, covering the maxillary teeth. MGP-PD 10170 is significantly affected by the pyrite oxidation and therefore not informative. Only MGP-PD 26816 preserves the lower jaw (labelled as MGP-PD 26817) isolated from the skull, but due to deformation, the contacts among the bones of the mandible are not perceivable. The best preserved skull is the one reported in Figure 3 in which the suture pattern - at least the dorsal one - can be almost completely reconstructed.

From an overall perspective, the skulls are relatively broad, presenting wide premaxillae, a curved maxillary contour at the level of the largest teeth, and diminutive orbits. However, the rostrum is quite elongate, the interorbital space is relatively narrow and the skull table is not expanded laterally and does not project posteriorly.

The anterior region of the rostrum is massive with an almost straight anterior margin of the premaxillae. The external nares are nearly rectangular, being slightly longer than wide. The external nares are slightly smaller than the orbit. As it is particularly clear in MGP-PD 26862, the posterolateral margin of the nares is elevated and the anterior region of the rim of the nares is flat and continuous with the external margin of the bone. All the skulls and the fragments of rostrum present the same suture pattern, described below. The nasals are clearly excluded from the posterior margin of the nares by the premaxillae as these bones are anteroposteriorly expanded at the level of the premaxillary-maxillary notch. The

premaxillary-maxillary suture is delineated by a pronounced embayment for reception of the third and fourth dentary teeth. At the level of the double caniniform tooth, the lateral maxillary margin is inflated. The nasals extend along most of the rostrum length. They taper anteriorly between the premaxillae, which send a short posterior process between the maxilla and nasal at the level of the first or second maxillary alveoli. The sutural pattern of the antorbital region is obscured in most of the specimens, but in two specimens, reported in Figure 3 and Figure 4 (A, B), which preserve the area clearly, the frontal separates the posterior tips of the nasals. The left side of NMB-Bc.6 indicates that the lacrimal tapers relatively far anteriorly at about the level of the sixth maxillary alveolus and therefore extensively contacts the posterolateral margin of the nasal. The prefrontal is not clearly distinguishable in any of the skulls.

The orbital region is characterized by a narrow interorbital width and small orbits. The anterior projection of the frontal is narrow (Figs 3, 4B). The interorbital region is marked by a well-delineated preorbital ridge passing through the frontal and following the anteromedial margin of the orbits on the prefrontal and lacrimal (Figs 3 and 4C). The interorbital region could seem different in Fig. 3A and Fig. 4C, but the different shape in Fig. 4C is due to a taphonomic effect. In fact, in Fig. 4C the anterior process of the prefrontal is detached and raised from the lacrimals surrounding it. The anterior-most margin of the orbits is formed by the lacrimal and is notched. This notch marks a depression, where the ornamentation is absent. The teardrop-shaped supratemporal fenestrae are well preserved in MGP-PD 28164 (Fig. 5), 26843, 26858 (Fig. 4C) and NMB-Bc.6 (Fig. 3). In NMB-Bc.6 and in MGP-PD 28164, the frontoparietal suture clearly penetrates the supratemporal fenestrae, preventing the postorbital from contacting the parietal on the skull table. The parietal is particularly wide between the supratemporal fenestrae, being almost as wide as each fenestra. The supraoccipital participates in the dorsal surface of the skull table and, even if the anterior part

of its suture with the parietal is not clearly visible in any of the specimens, it surely does not prevent the parietal from reaching the posterior margin of the table. The squamosal prongs are short and do not project far posteriorly nor laterally, as particularly evident in NMB-Bc.6.

The suture organization around the lower temporal fenestra is poorly visible in most of the specimens, because of the deformation they have been subjected to. The lower temporal fenestra seems narrow and elongate, but this may be an artefact of compression. The quadratojugal seems to form the posterior corner of this fenestra and extend along its dorsal margin, therefore excluding the quadrate from it. A small quadratojugal spine can be reconstructed to have been located near the dorsal level of the lower temporal fenestra, but it is not preserved in any specimen. The postorbital bar is barely visible (e.g. in MGP-PD 26814 and in NMB-Bc.6) because it is hidden by other bones due to deformation. The jugal projects far posteriorly, but does not prevent any lateral exposure of the quadratojugal, particularly evident in Figure 3. The small medial quadrate hemicondyle bears the notch for the foramen aëreum on its dorsal surface, as evident in most of the specimens (e.g. MGP-PD 26814, 26816, 26835, NMB-Bc. 6).

The palatal structure cannot be entirely reconstructed. The paired palatines comprise the median walls of the suborbital fenestrae. Their anterior part is never visible and thus the anterior extension of the suborbital fenestrae cannot be understood. The posterior part of the suborbital fenestrae are particularly well preserved in MGP-PD 26858 (Fig. 4D) and partially preserved in NMB-Bc.6. The palatines have parallel margins and there is no lateral flaring of each bone (Fig. 4D). The palatine-pterygoid suture is located well ahead of the posterior corner of the suborbital fenestra (Fig. 4D). The lateral edges of the palatines are parallel posteriorly, without producing a shelf. The pterygoid edge contributing to the posterior rim of the suborbital fenestra does not show any notch. The internal choanae open in the central region of the pterygoids. Their lateral margins form a collar, the pterygoid being depressed

lateral to it (particularly visible in MGP-PD 26844). The anterior extension of the ectopterygoid is unclear. The ventral ectopterygoid process is massive and does not project all the way to the tip of the pterygoid wing. Instead, it stops at more than half the distance, as visible in Figure 6D and NMB-Bc.6.

The mandibles are often associated, and articulated, with the skulls, but because of the strong deformation that they have suffered they are usually opened at the level of the contact between splenial and dentary (so that the external surface of the dentary and the internal surface of the splenial are exposed). Moreover, even if the bones are generally identified, most of the characters important for the identification are unperceivable. For example, the articular elements are very common among the Padua specimens, but the foramen aëreum is in most cases not visible. The mandibular symphysis is often visible – particularly well in Figure 6 (B, C, E, F) – and it extends to the 4th mandibular tooth. The surangular is pinched off anterior to the posterior extent of the retroarticular process in MGP-PD 26814. The retroarticular process is deeply concave and its tip projects posterodorsally.

The total number of teeth cannot be assessed. The maxillary teeth are at least 13 in MGP-PD 26844. When the dental pattern can be reconstructed, it emerges that the largest maxillary alveoli are the 4th and 5th, which are confluent. In MGP-PD 26815 and 26844, the 4th alveolus seems slightly smaller than the 5th (Fig. 2). The implication of this character will be discussed in the next section. The 6th tooth is considerably smaller than the 5th one. The 4th dentary alveolus is the largest, and its tooth is hosted in the notch corresponding to the maxilla-premaxilla suture. Even if the 3rd tooth is not preserved in any specimen, the maxillary notch is wide enough to host two dentary teeth in occlusion, corresponding to the 3rd and 4th confluent dentary alveoli. The occlusion is comparable to that of other species of *Diplocynodon* and can be reconstructed particularly well in MGP-PD 8648. In this specimen,

the maxilla is fractured in the two points in which the maxilla is notched, after the 4th mandibular tooth and after the 7th maxillary tooth.

Limited information can be gained from the postcranial elements. Among the Padua material, there are several portions of postcranial elements, but they are usually poorly preserved, or particularly altered. The vertebral column cannot be entirely reconstructed, because all the remains are fragmentary, and some parts of the vertebral column (i.e. the cervical vertebrae) are poorly preserved. The atlas is only preserved, but disarticulated, in NMB-Bc.6, which also preserves the axis and the third cervical vertebra in lateral view (Fig. 3C). Another axis is preserved (MGP-PD 26856), but its anterior crest is broken in both cases. The limbs and the pelvic and scapular girdle are also very fragmentary, even if in some cases still articulated. These elements were dissociated before burial of the animals as testified by the incompleteness also of NMB-Bc.6, which lacks the posterior trunk region. A similar pattern can be observed in the La Rochelle skeleton where only the left forelimb is still partially articulated and most of the dorsal osteoderms and the trunk vertebrae are missing. Noteworthy is the organization of the dorsal armor in the trunk region of NMB-Bc.6, where neural arches are visible, indicating the midline of the trunk (Fig. 7A, B). Herein is also visible a lateral osteoderm and it is therefore possible to clearly identify where the dorsal osteoderms stop. Each row of dorsal osteoderm can be thus reconstructed as containing six osteoderms (Fig. 7B). The dorsal midline osteoderms bear anterior process (Fig. 7C). The ventral armor is visible in lateral view in Figure 7 (D, E), where the ventral, bipartite osteoderms are clearly visible, and one ischium is also detectable (Fig. 7F). The distal portion of the shaft is greatly expanded; the maximum diameter of this expansion is oblique in position. The entire external surface of the ischium is somewhat convex. Each series of osteoderms overlaps the next series located posterior to it.

RESULTS

Provenance Analysis

Results are presented in Table 1 and Figure 8. The most radiogenic values were measured on the two samples from Purga di Bolca (average = 0.732). These differ significantly from the rest of the samples measured here (average = 0.711), including the two samples from Monteviale (MGP26855 and MGP26836), the samples from Basel and La Rochelle, and surprisingly the sample NHM-UK 2789 originally labelled as coming from Purga di Bolca.

Taxonomic Identification

The specific assignment to *Diplocynodon ratelii* by Brinkmann and Rauhe (1998), Del Favero (1999) and Pandolfi et al. (2016) is not accepted here, as discussed below. The organization of the sutures of the skull is basically the same as *D. tormis* from the Eocene, and *D. muelleri* from the Oligocene, of Spain (Buscalioni et al., 1992; Piras and Buscalioni, 2006). Besides being the same age, *D. muelleri* and the Monteviale crocodylians share the shape and proportions of the skull table, which bears teardrop-like supratemporal fenestrae (for *D. muelleri* see holotype in fig. 3 in Piras & Buscalioni, 2006), whereas in *D. tormis* they are more elliptical (see holotype in fig. 2 in Buscalioni et al., 1992). Moreover, the parietal between them is not as thin as in *D. tormis*, where each fenestra is twice as wide as the parietal. In the Monteviale specimens and *D. muelleri*, the parietal is about the same width as each fenestra. Piras and Buscalioni (2006) stated that *D. muelleri* shows a particularly short mandibular symphysis reaching the third mandibular alveolus. In this respect, the Monteviale specimens differ from it, as the symphysis reaches the fourth alveolus. However, in the holotype of *D. muelleri* (NMB-Spa.4), housed in Basel, the mandible is broken at the level of

the mandibular symphysis and it is therefore impossible to evaluate its extension. In *D. muelleri* NMB-Spa.73, the symphysis does not seem shorter than the one of the Monteviale specimens. A revision of the symphyses of all the specimens of *D. muelleri* is needed, but, at the state of the art, this character is not considered sufficient to distinguish between the Spanish species of *Diplocynodon* and the Monteviale crocodylian. The maxillary dentition pattern can be reconstructed only in two specimens from Monteviale (MGP-PD 26844 and MGP-PD 26815), which show the typical confluent 4th and 5th alveoli, but, differently from the other species of *Diplocynodon*, the 4th alveolus seems slightly smaller than the 5th (Fig. 2). Even if this character state is also found in *Asiatosuchus*-like crocodyloid taxa, the rest of the anatomy agrees with placement of these specimens in *Diplocynodon*. However, this feature could be only due to intraspecific variability and it seems more cautious to not consider it significant enough to attribute the material to a species separate from the others.

Phylogenetic Analysis

As in Martin et al. (2014), two analyses were carried out: including the two less complete species of *D. ungeri* and *D. elavericus* and excluding them. The topology and the nodal support metrics are in both cases consistent with the results of Martin et al. (2014). The *Diplocynodon* group has a Bremer (decay) index of one, but it is supported by seven unambiguous synapomorphies (characters 14, 33, 41, 68, 81, 148, 152 of Brochu et al., 2012). As in Martin et al. (2014), including the less complete species, the tree shows a polytomy at the basis of Diplocynodontidae (topology not reported herein), leaving unresolved the relationships among its members. The analysis excluding the less complete species retained 640 trees [consistency index (CI) = 0.3412; retention index (RI) = 0.8021]. For clarity of reading, the strict consensus tree excluding the less complete species (Fig. 9) has been simplified for some clades (i.e. Gavialoidea, Globidonta, and Crocodyloidea). The Monteviale

species is placed in a derived position, in a polytomy with *D. tormis* and *D. muelleri*, that is the sister group of *D. ratelii*.

DISCUSSION

Provenance Analysis

The present geochemical approach relies on a comparative assessment of the radiogenic strontium isotope values of two lignites from two localities. The $^{87}\text{Sr}/^{86}\text{Sr}$ composition of lignites for provenance purposes has not been widely used in paleontology and heterogeneity of the lignites may be problematic. Nevertheless, values obtained in the sample size available to fall into two groups. Our small sample size precludes statistical analysis. The strontium isotope values measured in the sediment depend on the age and lithology of the bedrock source. The high ratios measured in Purga di Bolca samples indicate a highly radiogenic source, possibly an old granitic substrate. On the other hand, the lignite from Monteviale was sourced from bedrock of a different composition. Results show that the lignite matrix surrounding the crocodile specimens housed in the Musée de La Rochelle, NMB Basel and NHM-UK London have strontium isotope ratios comparable to the samples analyzed from the Oligocene locality of Monteviale. It seems reasonable to consider these specimens as originating from Monteviale unless further analyses show otherwise.

Affinities of the Oligocene Crocodylians from Monteviale

After the revision of all the available crocodylian remains, it is clear that the Monteviale material belongs to a single species of *Diplocynodon*, as previously suggested (Rauhe and Rossmann, 1995; Kotsakis et al., 2004; Pandolfi et al., 2016). In fact, it shares the diagnostic characters of this genus: anterior process of the dorsal osteoderms, bipartite ventral

osteoderms (Fig. 7E), a pair of caniniform teeth hosted in confluent alveoli (maxillary teeth 4 and 5; Fig. 2), and the presence of a preorbital ridge (Fig. 3; Martin et al., 2014). This differs from *Asiatosuchus*-like crocodyloid taxa, which have a single enlarged fifth maxillary tooth and lack the preorbital ridge and the bipartite, ventral osteoderms (Delfino and Smith, 2009). Also, while both the Monteviale species of *Diplocynodon* and *Asiatosuchus* have small orbits compared to their skull size, the interorbital width in *Asiatosuchus* is much larger. The position of the frontoparietal suture does not seem to discriminate any affinity. In species of *Diplocynodon* and *Asiatosuchus germanicus*, the suture makes a deep entry in the supratemporal fenestra (Brochu, 1999) whereas in *A. grangeri* and *Asiatosuchus depressifrons*, the suture lies entirely on the skull table (Delfino and Smith, 2009; but see also Delfino et al., 2017, for the morphology of the oldest European *Asiatosuchus*). In the Monteviale specimens the suture makes a deep entry in the supratemporal fenestrae, a condition currently unknown in *Asiatosuchus* spp. The position of the foramen aëreum observed in the Monteviale species of *Diplocynodon* differs from that of *Asiatosuchus* and *Asiatosuchus*-like taxa for which the foramen aëreum is medially shifted. Here, this foramen is placed on the dorsal surface of the quadrate.

In *Asiatosuchus* the mandibular symphysis is long, extending at least to the sixth dentary alveolus (Leriche, 1899; Mook, 1940; Berg, 1966; Vasse, 1992; Delfino and Smith, 2009; Delfino et al., 2017). On the contrary, in species of *Diplocynodon* the symphysis extends between the third and the fourth dentary alveoli and is therefore shorter. The morphology exhibited by all the skulls from Monteviale clearly shows the condition found in species of *Diplocynodon*, extending the dentary symphysis to the fourth alveolus (e.g., MGP-PD 26843, MGP-PD 26844, MGP-PD 26814, MGP-PD 26815). The 3rd and 4th dentary alveoli, which are confluent in the species of *Diplocynodon*, are not visible in any case, but the corresponding maxillary notch is wide enough to host two teeth. The marked

premaxillary-maxillary notch is not diagnostic for *Asiatosuchus*, as it is present in several species of *Diplocynodon*. This feature develops during ontogeny, as observed for *D. hantoniensis* (Owen, 1849; Norell et al., 1994), *D. ratelii* (Berg, 1966; Brochu, 1999), *D. muelleri* (Piras and Buscalioni, 2006) and probably for most other species of *Diplocynodon*.

From a strictly osteological comparisons, there is no reason to support the option that *Asiatosuchus* was present at Monteviale (Franco and Piccoli, 1993) and the morphological uniformity of all the available material indicates that only one taxon is present. In fact, specimens which are only represented by anatomical elements not preserved on the types of *D. muelleri* or which, for preservational reasons, do not bear any diagnostic character are tentatively referred to the only species present in Monteviale, because they do not differ in morphology and size from *Diplocynodon*. This is also confirmed by the phylogenetic analysis which places the Monteviale crocodylian in a derived position nested among the other species of *Diplocynodon*. Indeed, all the remains from Monteviale presented in the literature should be ascribed to the genus *Diplocynodon*. This observation is also consistent with the known stratigraphic range of the genus *Asiatosuchus*, the latest unambiguous occurrence of which is from the Late Eocene (Bartonian) of Camburg, Germany (Vasse, 1992).

As far as the specific assignment is concerned, the previous specific attribution to *D. ratelii* (Brinkmann and Rauhe, 1998) and *D. cf. ratelii* (Pandolfi et al., 2016) is not confirmed. In fact, in *D. ratelii* the nasals clearly reach the external nares (Díaz Aráez et al., 2017), whereas in the studied material the nasals stop at least one centimetre away from the nares (Figs 3B, 4B, 5B). This is also confirmed by the phylogenetic analysis carried out, which retrieved the Monteviale specimen in a polytomy with the two Spanish species of *D. tormis* (Buscalioni et al., 1992) and *D. muelleri* (Piras and Buscalioni, 2006), forming together the sister group of *D. ratelii*. The morphology and the suture organization are very similar to those of *D. tormis* and *D. muelleri*. *Diplocynodon tormis* is an alligatoroid found in

the Eocene of Iberia (Buscalioni et al., 1992), whereas *D. muelleri* comes from the Oligocene of the same area (Piras and Buscalioni, 2006). These two species are very similar, showing no difference in the suture pattern of the skull. The general shape of the skull is asserted to be different by Piras and Buscalioni (2006), but this difference is most likely due to the fact that *D. muelleri* is dorso-ventrally compressed because of taphonomic processes, in a similar way of the *Diplocynodon* of Monteviale, whereas *D. tormis*, not being dorsoventrally compressed on a slab, preserved better the three-dimensional aspect of the skull, seeming slender. The main differences pointed out by Piras and Buscalioni (2006) concern the mandibular symphysis which they describe as particularly short in *D. muelleri*, reaching the third mandibular alveolus, and the palatal fenestrae which are described as particularly long in *D. muelleri*. Actually, a direct analysis of the *D. muelleri* holotype (NMB-Spa 4 T2) and another specimen (NMB-Spa 73) of this species, which are housed in Basel, indicated that these differences are not so evident. In fact, the holotype does not preserve the symphysis which is broken off and its palatal fenestrae are not clearly separated from the rest of the skull. The palatal fenestrae show a similar condition in NMB-Spa 73, but the symphysis is preserved and does not seem significantly less extended than in the Monteviale specimens, in which it reaches the 4th mandibular alveolus. Another difference between *D. muelleri* and *D. tormis* is related to the shape and proportion of the supratemporal fenestrae. The supratemporal fenestrae in *D. tormis*, in fact, are elliptical and wide, being twice as wide as the parietal between them, whereas in *D. muelleri*, they have a more teardrop-like shape and the parietal is wider between them. In this respect, the Monteviale specimens are more similar to *D. muelleri* than to *D. tormis*. Indeed, the supratemporal fenestrae are teardrop-like and the parietal is as wide as the fenestrae, as in *D. muelleri*. However, the skull table and the supratemporal fenestrae are known to change during ontogeny (Iordansky, 1973) and for this reason they are not widely used as important characters for taxonomy and phylogeny (Brochu,

1999). A careful revision of the species *D. tormis* and *D. muelleri* is currently needed to confirm the validity of both species ; indeed they may represent the same species at different ontogenetic stages. Currently, the Monteviale alligatoroid can be considered more similar to *D. muelleri* than to *D. tormis*.

Implications for Crocodylian Turnover

Comparative osteology suggests that no evidence exists for the presence of crocodyloids in the late Early Oligocene of Monteviale. Several European Eocene localities include multiple species within a given environment (Markwick, 1998; Martin, 2010). One hallmark example is the Messel oil shale locality (early Middle Eocene, MP 11, ca. 47 M.a.), which is composed of two generalist taxa of different size (the alligatoroid *Diplocynodon darwini* and the crocodyloid ‘*Asiatosuchus germanicus*’), one or two terrestrial predators (the sebecid *Bergisuchus dietrichbergi* and the eusuchian *Boverisuchus rollinatti*), and a diminutive tribodont (*Hassiacosuchus haupti*). This diverse assemblage thrived under the greenhouse climate during part of the Eocene. But climatic conditions drastically changed near the end of the Eocene (Zachos et al., 2001, Mosbrugger et al., 2005; Escarguel et al., 2008; Hérán et al., 2010); the progressive development of cooler conditions and the marked temperature decline at the very end of the Eocene most probably influenced the distribution of ectothermic taxa and contributed to the diversity decline observed across the EOB in crocodylian assemblages. After this event, the continental fossil record indicates only the presence of species of *Diplocynodon* (Antunes and Cahuzac, 1999; Piras et al., 2007). Due to their physiological constraints, crocodylians have been used as climatic proxies for inferring the latitudinal gradient of temperatures and hygrometry in the past (Markwick, 1998). Our results confirm this pattern: only one species exists in the Oligocene of Monteviale, namely a

species of *Diplocynodon*, a taxon broadly encountered in the freshwater ecosystems of that epoch.

CONCLUSIONS

The radiogenic strontium isotope ratio analysis performed herein revealed itself successful in ascertaining the provenance of the three previously unreported specimens *Diplocynodon* housed in collections in Basel, La Rochelle and London. This method can perhaps be applied to other specimens in general, and in particular to those specimens coming from north-east of Italy whose provenance is uncertain.

Following the morphological and taxonomic revision of all the available material, the crocodylians from Monteviale are assigned to a single species of the genus *Diplocynodon*, as previously proposed. There is indeed no evidence of *Asiatosuchus*-like taxa from the Oligocene of Monteviale, thus confirming a stratigraphic range for *Asiatosuchus*-like taxa restricted to the lower side of the Eocene-Oligocene boundary. Moreover, it seems likely that the only problematic specimen of *Diplocynodon* labelled as coming from Monte Bolca is actually coming from Monteviale. In fact, as said above, previous studies already underlined that nannofossils of the matrix of this specimen indicated a younger age than Eocene, compatible with Oligocene of Monteviale (Del Favero, 1999; Kotsakis et al., 2004). Furthermore, after our study, the morphological similarity between this single specimen labelled as coming from Monte Bolca and the Monteviale crocodylian is clear and thus the presence of a species of *Diplocynodon* in Monte Bolca seems to be unsubstantiated. The specific attribution *Diplocynodon* cf. *D. muelleri* is proposed, but a revision of the potential synonymy of the two Spanish species, *D. tormis* from the Eocene and *D. muelleri* from the Oligocene, is currently needed.

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FIGURE CAPTIONS

FIGURE 1. The Basel specimens of *Diplocynodon* from the Oligocene of Italy (NMB-Bc.6). **A** and **B** are two areas with some skeletal elements of one or two smaller individuals. Scale bar 5 cm. [planned for page width]

FIGURE 2. Details of the 4th and 5th maxillary alveoli of *Diplocynodon* from the Oligocene of Italy: MGP-PD 26844 (**A,B**) and MGP-PD 26815 (**C,D**). The two alveoli are confluent, but the 4th seems smaller than the 5th. Scale bar 1 cm. [planned for 2/3 of a whole page width]

FIGURE 3. Skull of *Diplocynodon* from the Oligocene of Italy: NMB-Bc.6 in dorsal view. **A**, dorsal view. **B**, interpretative drawing. **C**, interpretative drawing of the cervical area. **D**, interpretative drawing of the skull table. Scale bar 5 cm. **Abbreviations:** **Ax**, axis; **Ac**, axis crest; **Co**, occipital condilum; **Ex**, exoccipital; **Fr**, frontal; **Ic**, intercentrum; **Ju**, jugal; **Lna**, left neural arc; **Ma**, maxilla; **Na**, nasal; **Pa**, parietal; **Pm**, premaxilla; **Po**, postorbital; **SO**, supraoccipital; **Sq**, squamosal; **Qj**, quadratojugal; **Qu**, quadrate; **Rna**, right neural arch; **Tv**, third cervical vertebra. [planned for 2/3 of a whole page width]

FIGURE 4. Selection of skulls of *Diplocynodon* from the Oligocene of Italy. **A**, MGP-PD 26850 in dorsal view. **B**, interpretative drawing of MGP-PD 26850. **C**, MGP-PD 26858 in dorsal view. **D**, interpretative drawing of the ventral view of MGP-PD 26858, showing the palatines (**Pa**) with parallel margins and the suture between palatines and pterygoids (**Pt**) located well ahead of the posterior corner of the suborbital fenestra. Scale bar 2 cm.

Abbreviations: **Fr**, frontal; **Ma**, maxilla; **Na**, nasal; **Pm**, premaxilla. [planned for 2/3 of a whole page width]

FIGURE 5. *Diplocynodon* from the Oligocene of Italy. **A**, MGP-PD 28164 in dorsal view. **B**, interpretative drawing of the rostrum. **C**, interpretative drawing of the skull table. Scale bar 1 cm. **Abbreviations:** **Fr**, frontal; **Ma**, maxilla; **Na**, nasal; **Pa**, parietal; **Pm**, premaxilla; **Po**, postorbital; **Sq**, squamosal. [planned for 2/3 of a whole page width]

FIGURE 6. *Diplocynodon* from the Oligocene of Italy. **A**, MGP-PD 26843 in dorsal view. **B**, MGP-PD 26843 in ventral view. **C**, interpretative drawing of the mandibular symphysis of MGP-PD 26843. **D**, right pterygoid wing in ventral view (MGP-PD 31998) showing the contact between pterygoid (**Pt**) and ectopterygoid (**Ec**). **E**, MGP-PD 26815 in ventral view. **F**, interpretative drawing of the mandibular symphysis of MGP-PD 26815. Scale bar 2 cm. [planned for 2/3 of a whole page width]

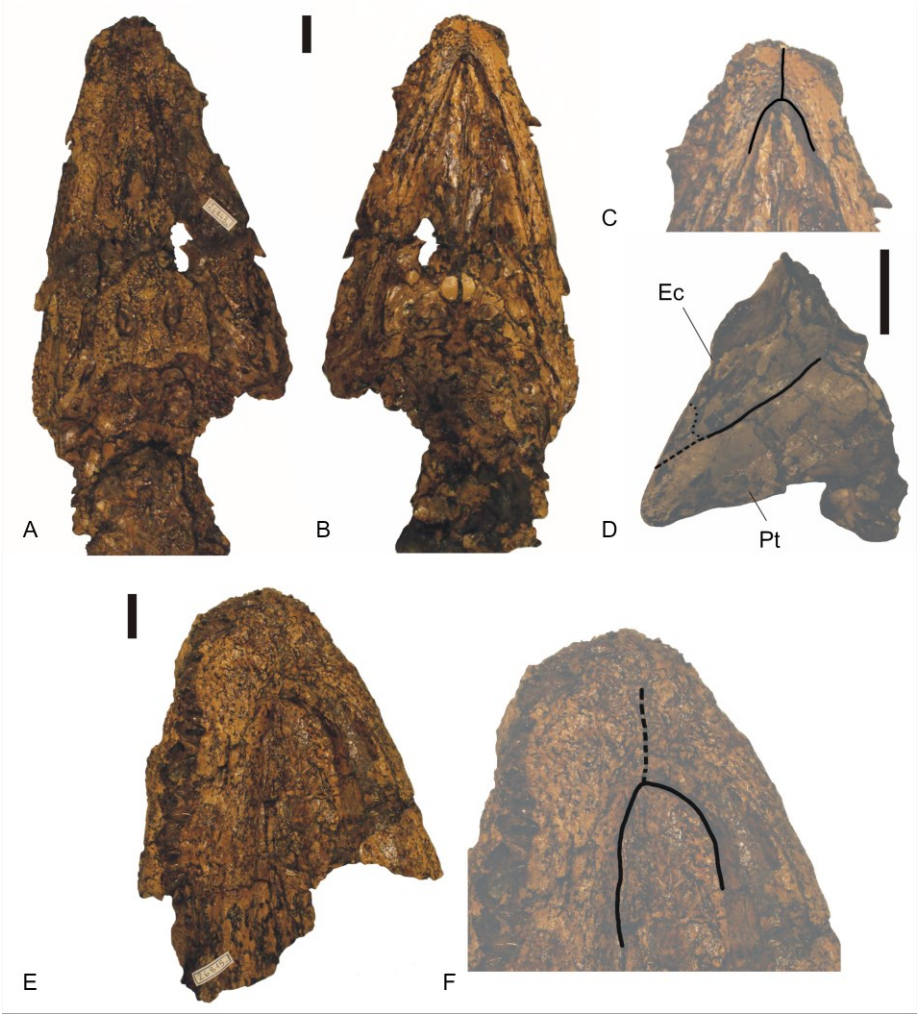
FIGURE 7. *Diplocynodon* from the Oligocene of Italy. **A**, dorsal armor of NMB-Bc.6. **B**, interpretative drawing of the dorsal armor of NMB-Bc.6, showing that each row of it was composed by three osteoderms per side, so six osteoderms in total. **C**, dorsal osteoderm from NMB-Bc.6, with the typical anterior process. **D**, part of a lumbar column (MGP-PD 27999 and 26854) with ventral osteoderms. **E**, detail and interpretative drawing of a ventral, bipartite osteoderm from MGP-PD 27999. **F**, detail of an ischium from MGP-PD 27999. Scale bar 5 cm. [planned for 2/3 of a whole page width]

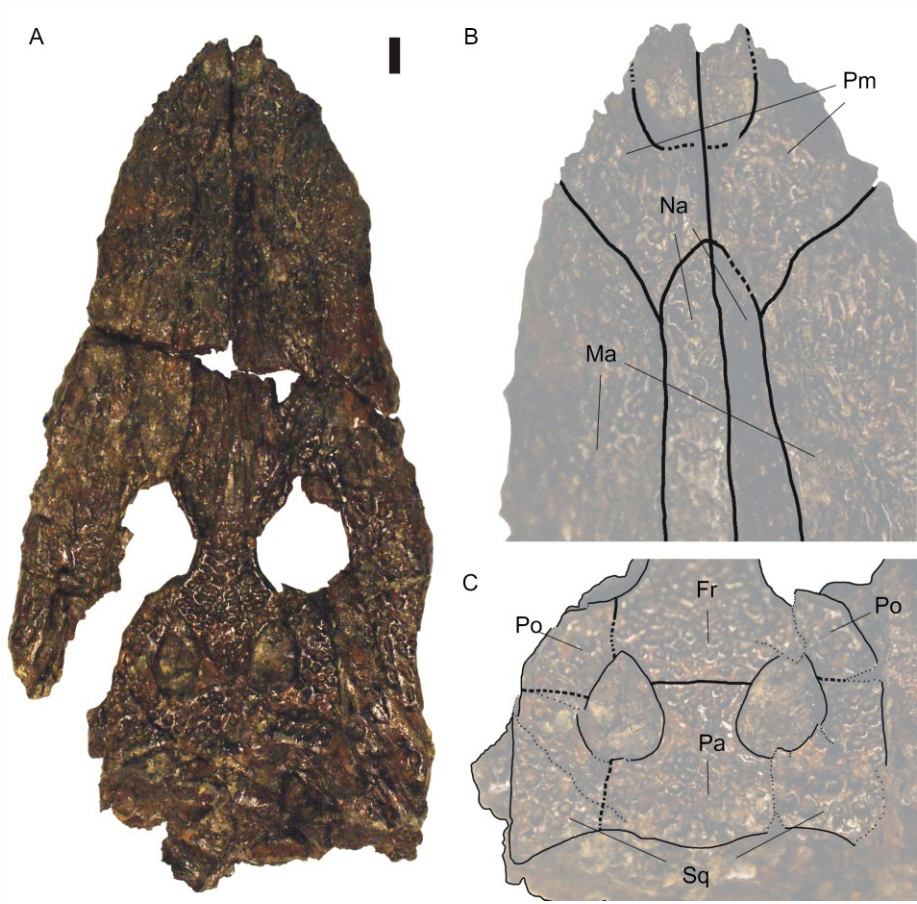
FIGURE 8. Comparison of strontium isotope ratios ($\text{Sr}^{87/86}$) of selected lignites sampled in the embedding matrix of crocodylian skeletons housed in various institutions. [planned for column width]

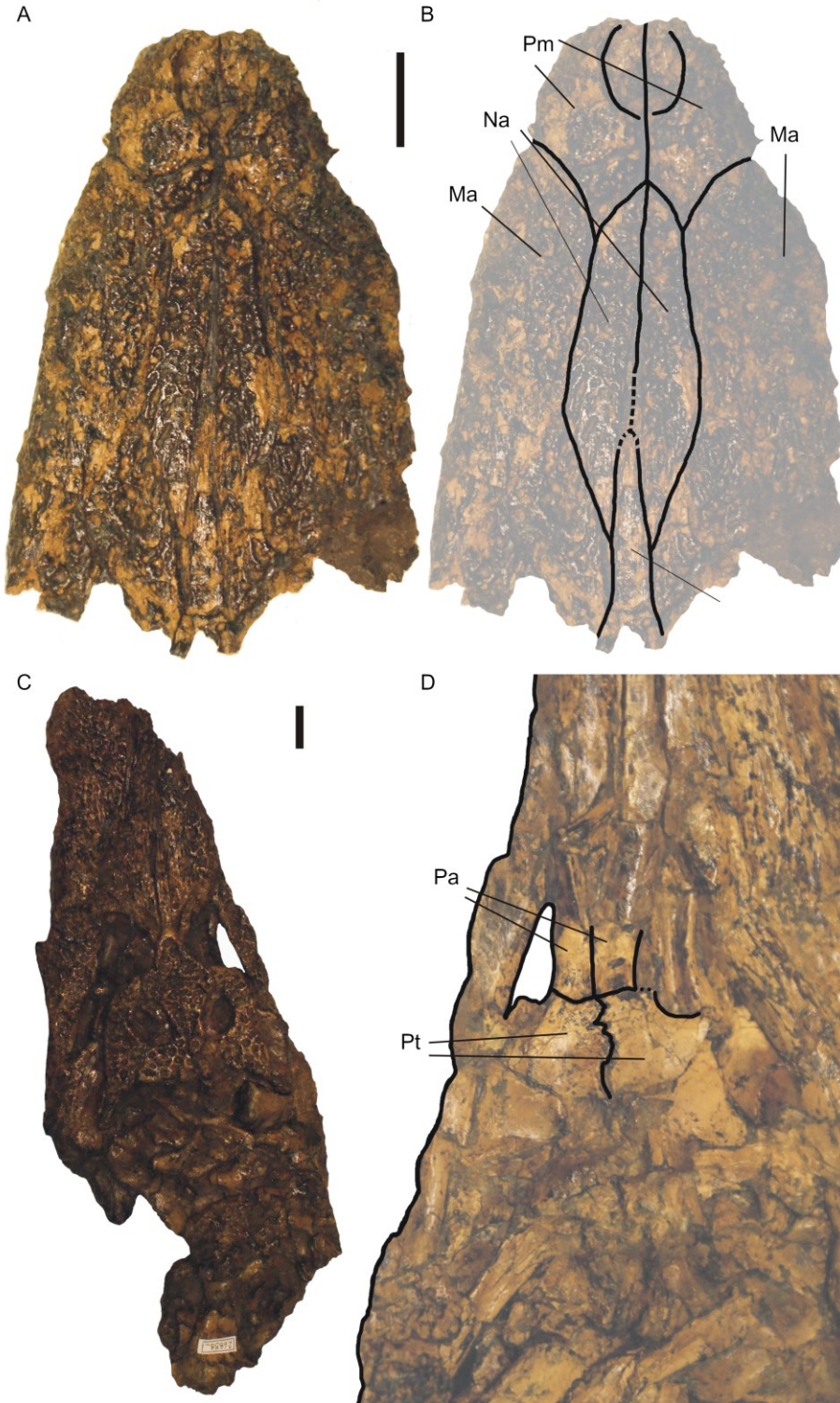
FIGURE 9. Strict consensus tree resulting from the inclusion of the *Diplocynodon* from Monteviale, Italy in the character matrix of Martin *et al.* (2014). The Monteviale taxon is placed in a derived position within the clade of *Diplocynodon* in a polytomy with *D. muelleri* and *D. tormis*. [planned for column width]

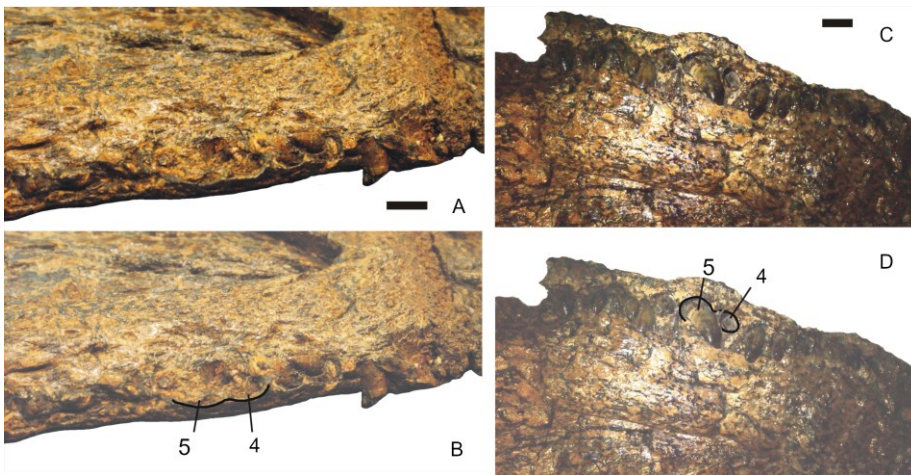
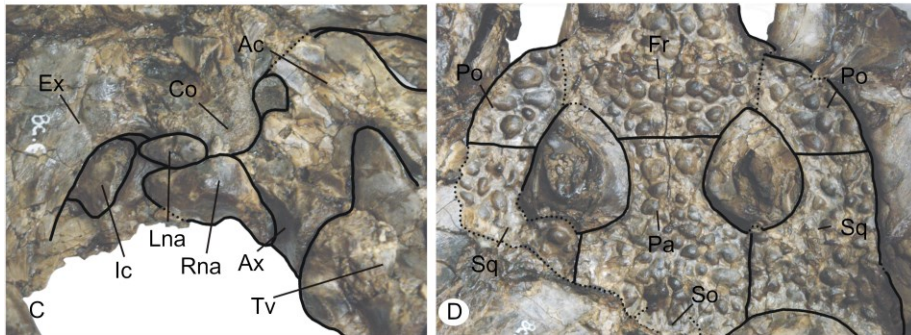
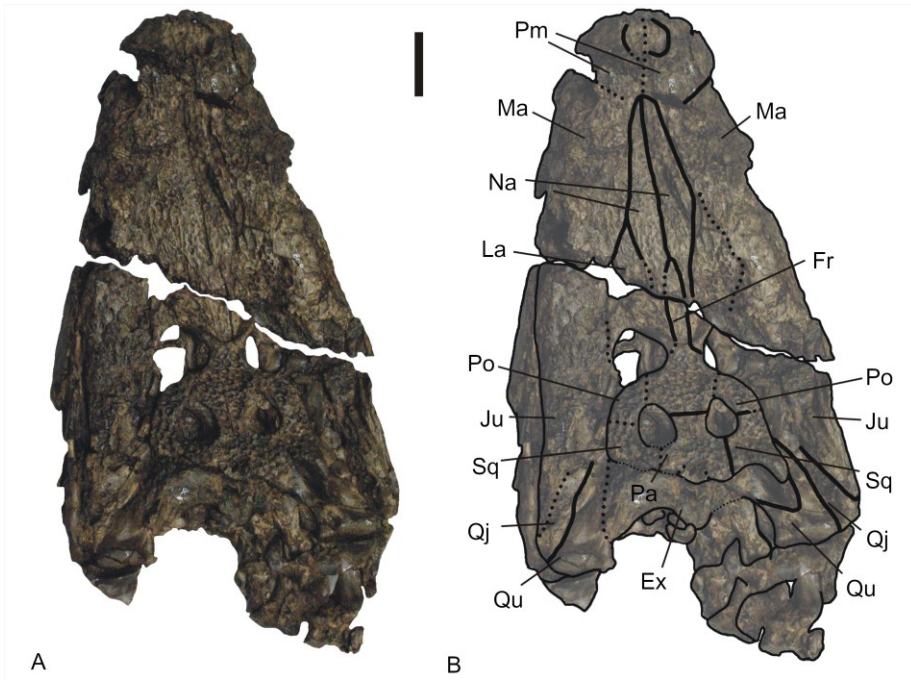
TABLE 1. Strontium isotope ratios ($^{87}/^{86}$) of selected lignites sampled in the embedding matrix of crocodylian skeletons housed in various institutions.

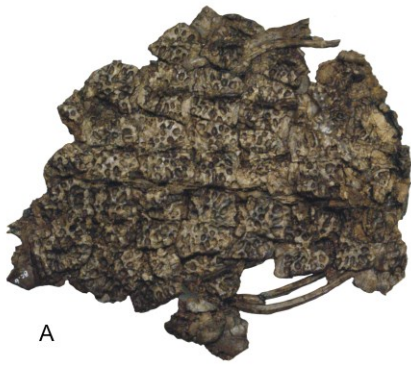
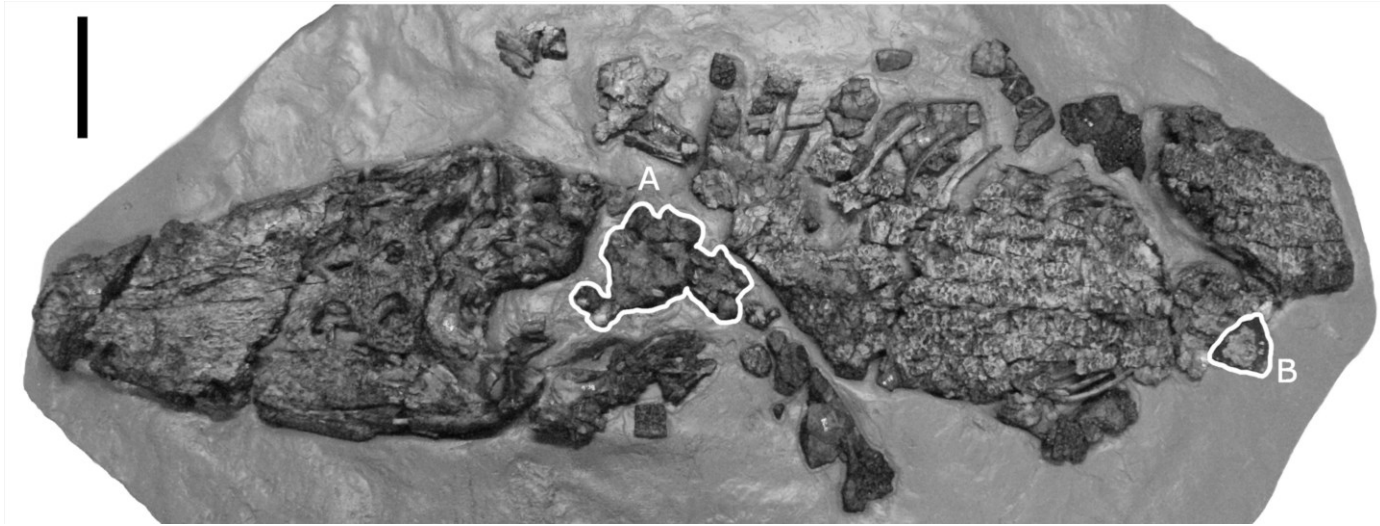
Provenance	Sample	Mean $^{87}\text{Sr}/^{86}\text{Sr}$	2SD
unknown	NHM Basle	0.709	0.001
unknown	La Rochelle	0.714	0.003
unknown	NHMUK PRV 2789	0.710	0.002
Monteviale	MGP26855	0.709	0.002
Monteviale	MGP 26836	0.710	0.002
Purga di Bolca	1	0.734	0.008
Purga di Bolca	2	0.731	0.007







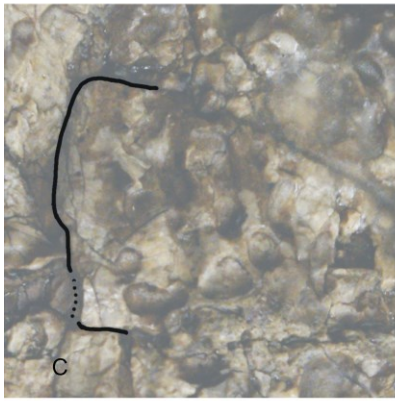




A



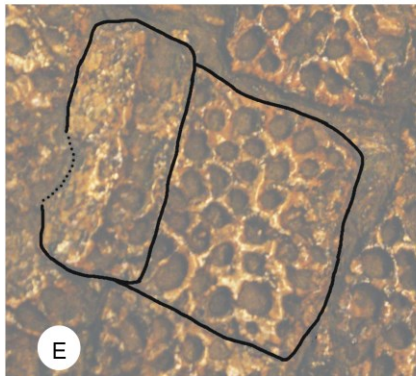
B



C



D



E



F

