

A new species of *Diplocynodon* (Crocodylia, Alligatoroidea) from the Late Eocene of the Massif Central, France, and the evolution of the genus in the climatic context of the Late Palaeogene

JEREMY E. MARTIN*

CNRS, UMR 5125, PaléoEnvironnements et PaléobioSphère, Université Lyon 1, Villeurbanne, Université de Lyon, F-69622, Lyon, France

(Received 18 September 2008; accepted 27 April 2009; First published online 15 January 2010)

Abstract – The genus *Diplocynodon* is widely recorded in Europe from Early Eocene up to Middle Miocene times. A fragmented but almost complete skull of a new species of *Diplocynodon* is reported from the Late Eocene locality of Domérat, northern border of the Massif Central (Allier), France. The present skull provides an important basis for comparison with other members of the genus and complements a fossil record full of gaps despite the large number of vertebrate localities spanning the Cenozoic. The new taxon occurs at a key period for climate evolution with conditions marking the transition from a greenhouse to an icehouse world. The response of crocodylian assemblages to this climatic shift is discussed in light of evidence for their decline in diversity from the Eocene period onward.

Keywords: Crocodylia, *Diplocynodon*, Eocene, Oligocene, climate.

1. Introduction

During Cenozoic times, European freshwater ecosystems hosted a number of crocodylian taxa. Many of them were ubiquitous across Europe and reported from Palaeocene and Eocene strata. Among these, the basal alligatoroid genus *Diplocynodon* has the longest stratigraphic record, ranging from the Early Eocene to the Middle Miocene. This genus has been recognized for a long time, its first description dating from the mid-1800s with the first report of *Diplocynodon ratelii* from the Early Miocene of Saint-Gérand-le-Puy in Allier, France (Pomel, 1847). Since then, more species were erected, and the last comprehensive review of the genus accepted eight species (Berg, 1966). Recently, reports or attempts at taxonomic clarification were also presented (Vignaud *et al.* 1996; Ginsburg & Bulot, 1997; Brinkmann & Rauhe, 1998; Del Favero, 1999; Hua, 2004), and some efforts have concentrated on including species of *Diplocynodon* into a phylogenetic framework (Buscalioni, Sanz & Lourdes, 1992; Brochu, 1999; Piras & Buscalioni, 2006). Despite that, the genus *Diplocynodon* still encompasses a fairly large number of species; because of this and its long stratigraphic record, the picture of its evolution is rather far from being fully resolved. A very large number of vertebrate-bearing localities are recorded throughout the Cenozoic, but few have yielded complete crocodylian remains, which would provide sufficient basis for taxonomic assessment. Many crocodylian remains are fragmentary and it is

questionable whether efforts have concentrated mostly on small remains, namely mammal or herpetofaunistic assemblages to the detriment of larger vertebrates. Nevertheless, crocodylian skull fragments or isolated teeth and osteoderms are not commonly diagnostic beyond an ordinal level. Depending on the energetic nature of a deposit, such remains may still be abundantly recovered through sieving but will not yield sufficient taxonomic information in comparison to mammal teeth.

Thus, any additional material from a new or already known locality is of importance, as remains identified to the species level present a less complete stratigraphic picture among crocodylians than among diminutive mammals. Despite this fact, their fossil record is potentially promising, thanks to a depositional environment offering favourable conditions to their preservation. Moreover, in exceptional cases, articulated and exquisitely preserved specimens were recovered from Germany (Messel and the Geiseltal) and Italy (Monte Bolca). Such Lagerstätten provide excellent snapshots of diversity, but other types of preservation including accumulation in river channels are nevertheless informative. Landmark localities having yielded the best material are regionally limited to a handful of outcrops for a given time interval. This highlights one of the major problems regarding the continental fossil record: it is discontinuous, therefore, any new fossiliferous locality is of importance.

The present report describes a new *Diplocynodon* taxon from the terminal Eocene of Massif Central, France. The locality of Domérat, Allier (Fig. 1), which has yielded it, was dated on its mammal assemblage to the Mammal Palaeogene level MP18–20 (Meloux *et al.* 1996).

Present address: Laboratoire de géologie, Université de Corse, 20250 Corté, France

*E-mail: martin@univ-corse.fr

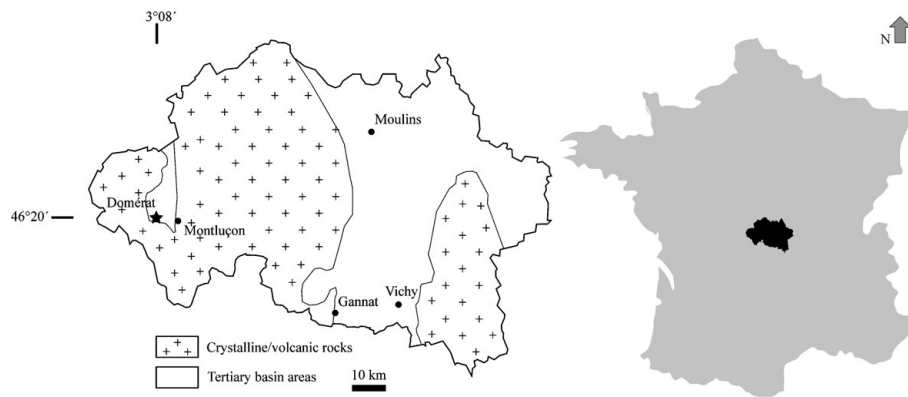


Figure 1. Geographic position of the locality of Domérat, Massif Central in the 'département de l'Allier', France.

Despite several mentions from North America (Mook, 1960; Grandstaff *et al.* 1992; Parris *et al.* 1997) and from Asia (Efimov, 1988; Guanbang & Guikun, 1993), the genus *Diplocynodon* is, after reappraisal, thought to be endemic to Europe (Brochu, 1999; Piras & Buscalioni, 2006) and is known to have survived important climatic changes from a greenhouse Palaeogene to an icehouse period in the early Neogene. A change in crocodylian faunal composition was observed during this time interval. Ecosystems hosting several taxa shifted to ecosystems with a single taxon. However, any link between these observations remains unclear, and hypotheses for crocodylian faunal turnover at this period will be discussed below.

2. Geological setting

The *département de l'Allier* has rich vertebrate-bearing localities, including the Lower Miocene vertebrate fauna of Saint-Gérard-le-Puy in the Limagne basin, from where the holotype of *Diplocynodon* was recovered (Pomel, 1847). The older locality of Domérat is located in the western part of Allier in the smaller Montluçon–Domérat basin, separated from the Limagne basin by the northern crystalline and volcanic extension of the Massif Central horst (Fig. 1). The establishment of these basins is linked to the regional tectonic activity. The Domérat–Montluçon basin is delimited on its eastern margin by the Cher River fault with a N–S direction; therefore the basin follows this orientation.

A brief sedimentary study was provided by Thiry *et al.* (1983), who characterized successions of palaeopedogenetic levels and detrital deposits. Among these deposits, lenses of dark green clay occur and have yielded the Late Eocene vertebrate fauna of Domérat. According to Meloux *et al.* (1996), the mammal assemblage, with *Palaeotherium*, *Plagiolophus*, *Anoplotherium*, *Xiphodon* and *Amphimeryx*, indicates a Ludian (Middle Priabonian) age corresponding to the MP18–MP20 reference level of the mammalian biochronological scale for the Palaeogene of Europe (BiochroM, 1997).

Mammal remains reported from this locality essentially consist of isolated teeth, as well as rolled and often incomplete bones. The recovery of pebbles led Meloux *et al.* (1996) to suggest a flash-flood type of burial, which would have trapped the mammals at a drinking spot in a marshy environment. Vertebrate remains were eventually transported and sorted. The present report of a *Diplocynodon* skull does not seem to fit such a scenario. Despite poor preservation, it is complete and the recovery of bones in connection with the associated mandible is not in agreement with any long transport. The bones sometimes appear to be heavily weathered and turned into a yellowish oxidized dust. It is possible, however, that mammal bones were transported and sorted, as the depositional environment may correspond to a river channel. In any case, the presence of the complete *Diplocynodon* skull provides evidence that fossil remains recovered from that locality underwent different taphonomic processes.

Institutional abbreviations: Rhinopolis – Association Rhinopolis, Gannat, Allier, France; BMNH – British Museum of Natural History, London.

3. Systematic palaeontology

CROCODYLIA Gmelin, 1789 (*sensu* Martin & Benton, 2008)

EUSUCHIA Huxley, 1875

ALLIGATOROIDEA Gray, 1844

DIPLOCYNODONTIDAE Hua, 2004

Genus *Diplocynodon* Pomel, 1847

Type species. *Diplocynodon ratelii* Pomel 1847.

Diplocynodon elavericus sp. nov.
Figures 2–9

Holotype. Rhinopolis B3, an almost complete skull with mandibular fragments and some osteoderms.

Etymology. 'elavericus' refers to the Latin name of the Allier River: elaver. Note that Bravard (1843) used '*Crocodylus elaveris*' to designate various crocodylian remains from Allier but did not provide any description, nor did he figure any specimens. As Vaillant (1872) pointed out, this early mention cannot be considered as having any right of priority over *Diplocynodon ratelii*, given the absence of a description or figure. '*Crocodylus elaveris*' should be considered as a *nomen nudum*. Here, to prevent any ambiguity, a slightly different species name is chosen for the new taxon described below.

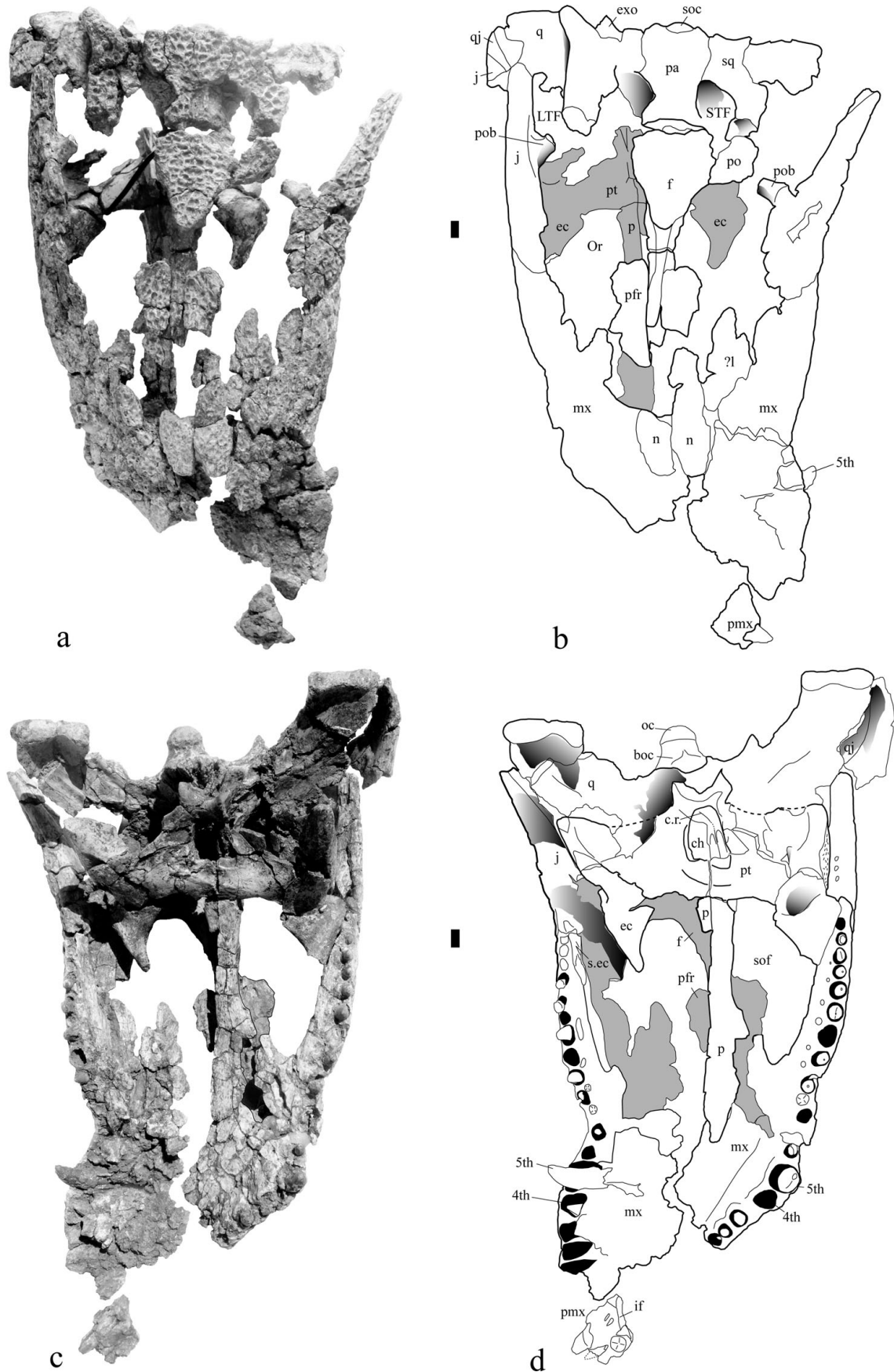


Figure 2. The skull of *Diplocynodon elavericus* (Rhinopolis B3) in dorsal (a, b) and ventral (c, d) views. Abbreviations: boc – basioccipital; ch – choana; c.r. – choanal recess; ec – ectopterygoid; exo – exoccipital; f – frontal; if – incisive foramen; LTF – lower temporal fenestra; j – jugal; l – lacrimal; mx – maxilla; n – nasal; oc – occipital condyle; Or – orbit; p – palatine; pa – parietal; pfr – prefrontal; po – postorbital; pob – postorbital bar; pt – pterygoid; pmx – premaxilla; q – quadrate; qj – quadratejugal; s.ec. – suture for ectopterygoid; sof – suborbital fenestra; sq – squamosal; STF – supratemporal fenestra; soc – supraoccipital; 4th, 5th – fourth and fifth maxillary tooth. Scale bar represents 1 cm.

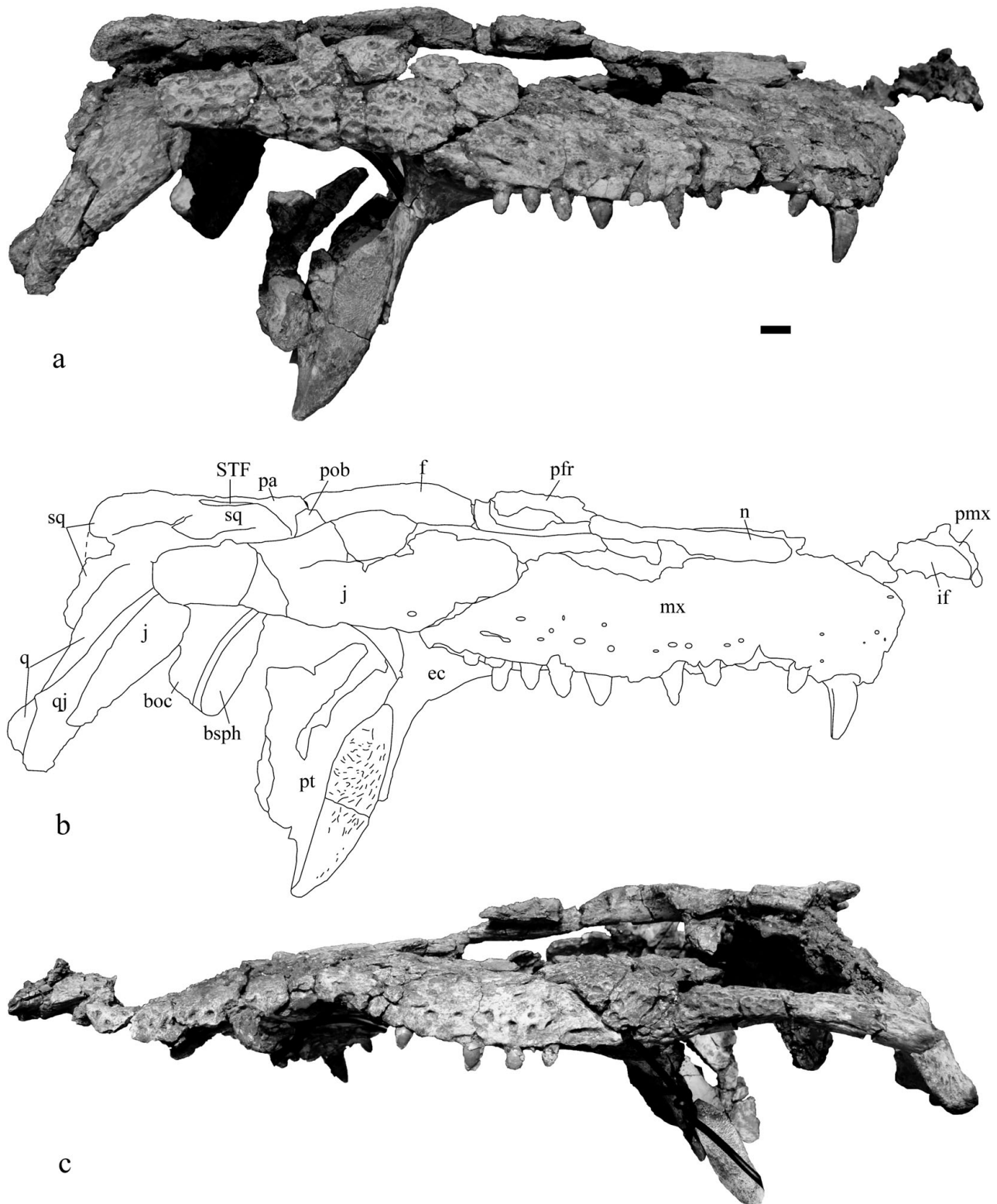


Figure 3. The skull of *Diplocynodon elavericus* (Rhinopolis B3) in right lateral (a, b) and left lateral (c) views. boc – basioccipital; bsph – basisphenoid; ec – ectopterygoid; f – frontal; if – incisive foramen; j – jugal; mx – maxilla; n – nasal; pa – parietal; pfr – prefrontal; pmx – premaxilla; pob – postorbital bar; pt – pterygoid; q – quadrate; qj – quadratojugal; sq – squamosal; STF – supratemporal fenestra. Scale bar represents 1 cm.

Locality and horizon. Middle Priabonian, Late Eocene of Domérat, Allier, France.

Diagnosis. Among the genus *Diplocynodon*, elongated quadrate rami and a pterygoid–palatine suture located at the posterior angle of the suborbital fenestra are autapomorphic

for *D. elavericus*. This taxon differs from *D. hantoniensis* in lacking an elevated rim around the supratemporal fenestra and by having a horizontal skull table and a slender palatine projection in the maxillae. It also differs from *D. tormis*, *D. muelleri* and *D. darwini* in having a longer rostrum. The

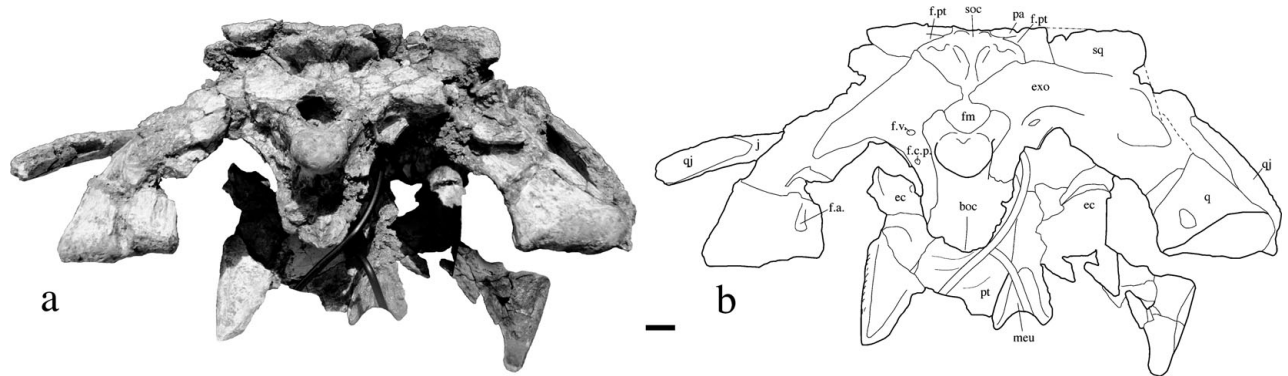


Figure 4. The skull of *Diplocynodon elavericus* (Rhinopolis B3) in occipital (a, b) view. Abbreviations: boc – basioccipital; ec – ectopterygoid; exo – exoccipital; f.a. – foramen aëreum; f.c.p. – foramen caroticum posterius; fm – foramen magnum; f.pt – posttemporal fenestra; f.v. – foramen vagi; j – jugal; me – median eustachian foramen; pa – parietal; pt – pterygoid; q – quadrate; qj – quadratojugal; soc – supraoccipital; sq – squamosal. Scale bar represents 1 cm.

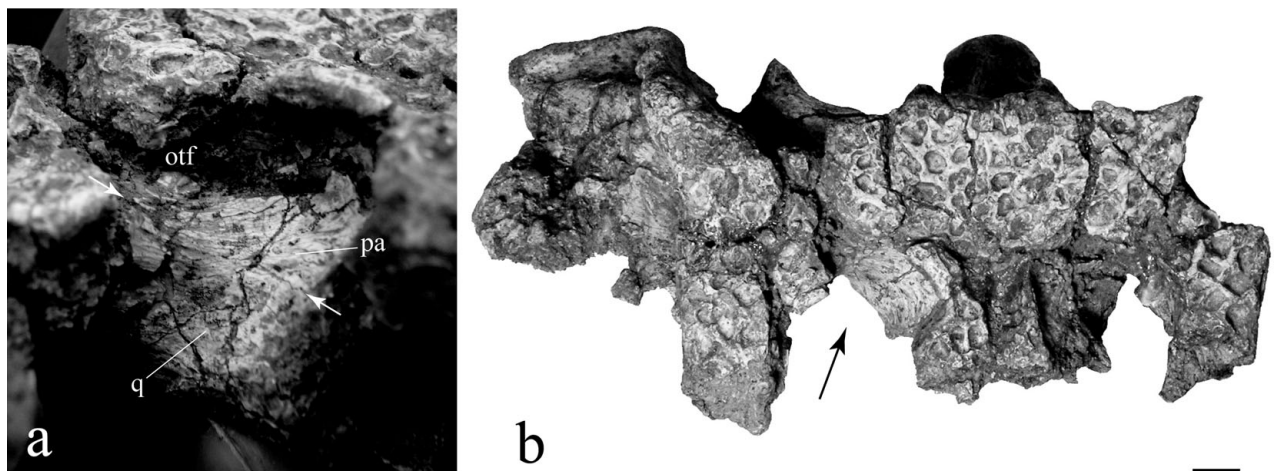


Figure 5. The posterior skull table of *Diplocynodon elavericus* (Rhinopolis B3): (a) detail of the right supratemporal fenestra in anterior view. The white arrows delimit the parietal–quadrate suture; (b) dorsal view of the skull table with the black arrow pointing to the detailed region in (a). Abbreviations: otf – orbitotemporal foramen; pa – parietal; q – quadrate. Scale bar represents 1 cm.

rostrum of *D. elavericus* is, however, shorter than the rostrum of *D. gervaisi*, *D. ratelii* and *D. styriacus*.

4. Description

Preservation. The remains of a single specimen were recovered in loose connection. Bones were not plastically deformed, but the skull is heavily fragmented and all the bones are displaced along cracks and sutures where they are cemented by clay. Therefore, the clay keeps the skull elements in a conformation close to the original one, but most of the contact between the bones has been destroyed either by clay swelling or during the excavation. Bones were prepared piece by piece and glued back together when connections were found. However, most of the medial and anterior region of the rostrum is missing. In some places, the bone and teeth are altered and turn into a yellowish powder.

Description. The premaxilla is very fragmentary. The only recognizable piece is an anterior fragment of the left premaxilla bearing two teeth. The anteriormost margin is straight. In ventral view, the first alveolus is broken and may have been small. A large occlusal pit separates the first alveolus from the second alveolus. The third alveolus is almost three times larger than the second. The premaxilla is then broken behind that alveolus. A foramen perforates

the base of the alveolar wall. The margin of the external naris is smooth and vertical. The anterior extension of the incisive foramen is visible and was excluded from the tooth row margin.

Both maxillae are preserved but their palatal suture and the connection with the nasal is not preserved. The suture with the premaxilla is preserved on the right maxilla and does not show a marked notch for the passage of the mandibular caniniform dentition. Each maxilla bears 17 alveoli. The largest alveoli are as in other *Diplocynodon*, the fourth and fifth. At their level, the lateral margin of the maxilla is convex, and then posteriorly behind the sixth alveolus, a constriction marks the lateral margin of the bone. The occlusion pattern is well discernable from the presence of pits along the tooth row. The first pit is visible between the sixth and seventh alveoli. This is the deepest of all. Pits are then observed between the seventh and eighth up to the last alveoli. However, their position in the anterior portion progressively shifts from a nearly interfingering position to a complete medial position in the posterior region. Moreover, from the eleventh to the fifteenth alveolus, the pits turn into a groove medial to the tooth row. Small foramina perforate this groove. The maxilla forms most of the lateral and all the anterior margin of the suborbital fenestra. In this lateral margin, the maxilla is completely vertical. A foramen pierces this lateral wall. Posteriorly, the maxilla does not send any

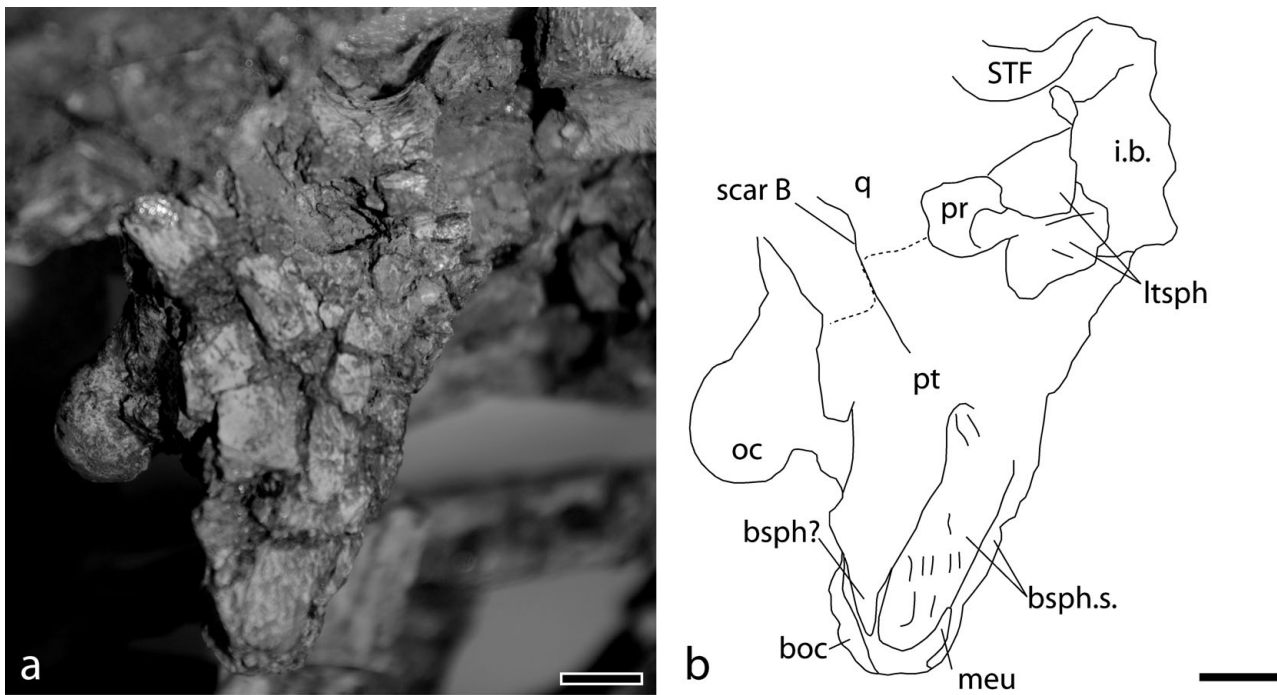


Figure 6. The braincase of *Diplocynodon elavericus* (Rhinopolis B3) in right lateral view. Abbreviations: boc – basioccipital; bsph – basisphenoid; bsph.s. – suture for basisphenoid; i.b. – internal braincase; Itsph – laterosphenoid; meu – median eustachian foramen; oc – occipital condyle; pr – prootic; pt – pterygoid; q – quadrate; scar B – muscle scar B of Iordansky (1973); STF – supratemporal fenestra. Scale bar represents 1 cm.

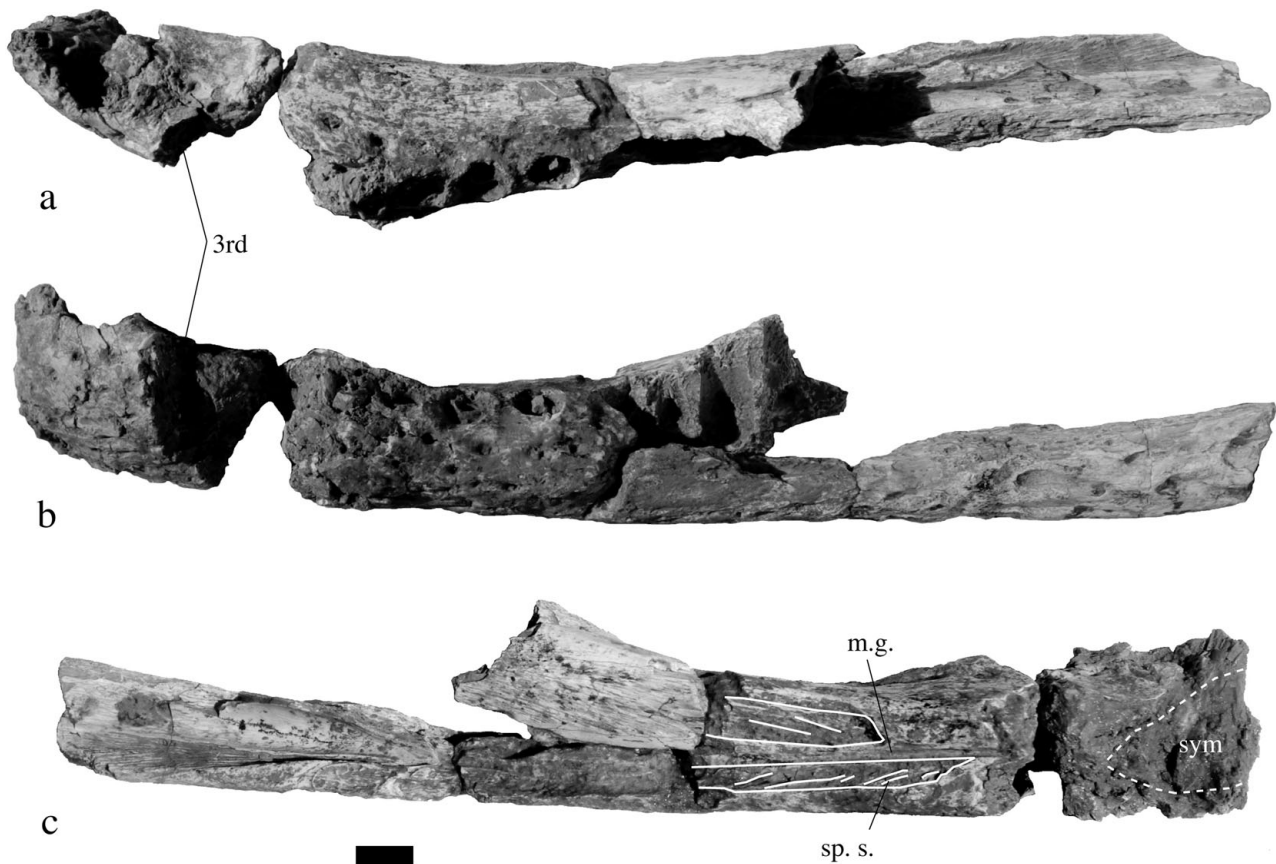


Figure 7. The left dentary of *Diplocynodon elavericus* (Rhinopolis B3) in occlusal (a), lateral (b) and medial (c) views. Abbreviations: m.g. – meckelian groove; sp. s. – splenial symphysis; sym – symphysis; 3rd – position for third confluent alveolus. Scale bar represents 1 cm.

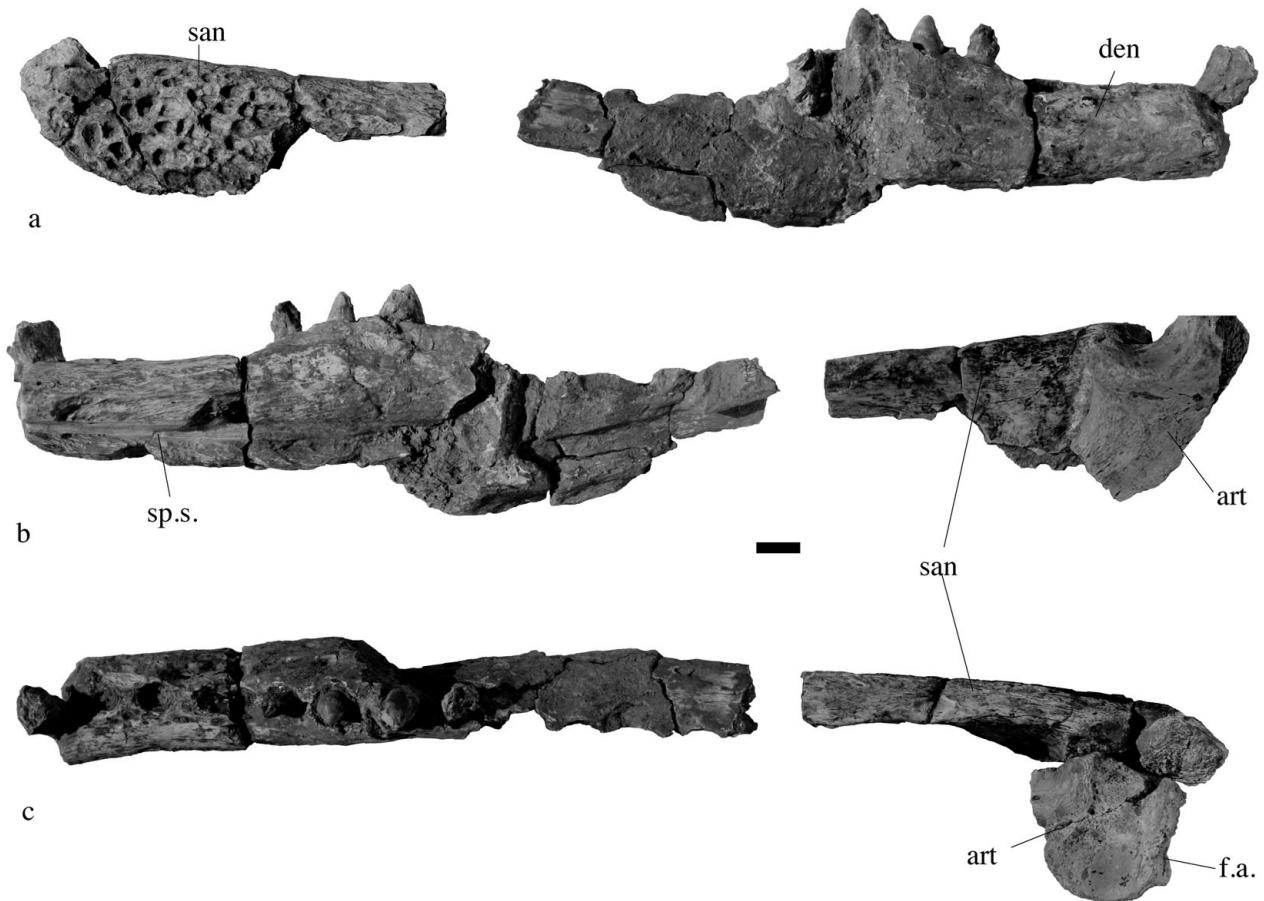


Figure 8. The right dentary of *Diplocynodon elavericus* (Rhinopolis B3) in lateral (a), medial (b) and occlusal (c) views. Abbreviations: art – articular; den – dentary; f.a. – foramen aëreum; san – surangular; sp.s. – suture for splenial. Scale bar represents 1 cm.

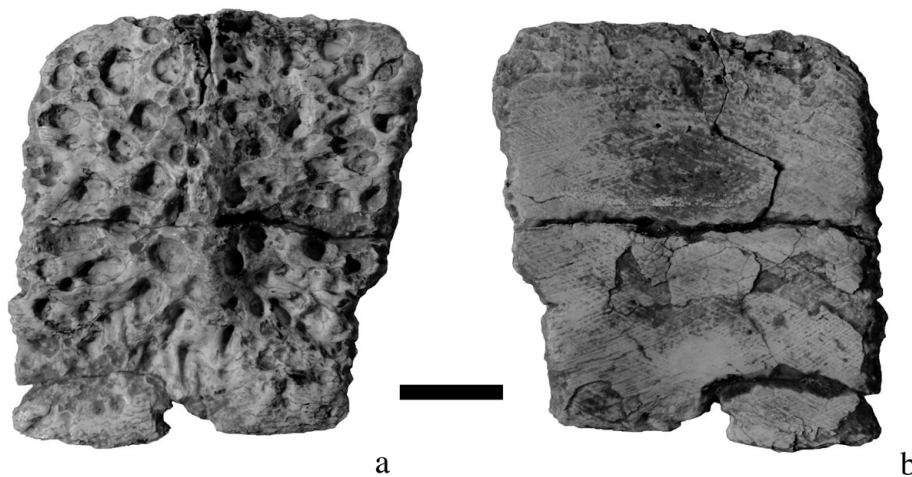


Figure 9. Dorsal osteoderm of *Diplocynodon elavericus* (Rhinopolis B3) in dorsal (a) and ventral (b) views. Scale bar represents 1 cm.

outgrowth between the tooth row and the ectopterygoid. Instead, the ectopterygoid is adjacent to the last two alveoli. The right maxilla offers some information about the medial wall of the cavichonchal recess. However, it is extensively fractured and further preparation could not be carried out. The cavichonchal recess is deep and its medial wall is smooth. Despite the fractures, no caecal recesses could be detected near the ventral lamina of the maxilla.

The nasal is very fragmentary and the few available fragments do not present any connection with the bones of the rostrum. However, given the conformation of the maxilla, the

nasals seem to have been excluded from the external naris. The nasals seem to expand laterally near their mid-region. They are dorsally sculptured with small circular pits.

The lacrimals are very fragmentary and their anterior extension is impossible to assess.

The prefrontals are divided by the frontal. They are elongate and form the anteromedial margin of the orbits. Laterally, they are slightly inflated near the sutural region with the lacrimal.

The frontal sends a long anterior and finely sculptured process onto the rostrum. From what is presently preserved,

this process attains the anterior level of the prefrontal extension. This process descends gently from the skull table but is not separated from it by a preorbital ridge. The skull table portion of the frontal is completely flat and sculptured with large circular and shallow pits. The frontal seems to enter into the supratemporal fenestrae. No contact between parietal and postorbital seems to occur.

The parietal forms the median and posterior region of the skull table. It is completely flat and shows the same patterns of sculptures on its dorsal surface. Between the supratemporal fenestrae, the bone margins are not straight but constricted. There is no ridge elevated along their rim. On the left side, the anteriormost margin of the supratemporal fenestra presents a fossa formed by the parietal. The parietal forms the ventral portion of the orbitotemporal foramen, therefore preventing the ascending process of the quadrate from attaining this foramen. The parietal contacts the squamosal lateral to that foramen. The posterior margin of the skull table is uneven and marked by two small processes.

The jugal forms the lateral boundary of the infratemporal fenestra. It is heavily sculptured on its dorsal surface with deep pits. It also participates in the anterolateral boundary of the orbit where it projects over the maxilla as a thin plate. The jugal contributes to the postorbital bar by sending a process, which is inset from the dorsal margin of the bone. While it is inset, the process is, however, continuous with the medial smooth margin of the jugal. Ventrally, the suture for reception of the ectopterygoid does not extend onto the posterior jugal rod. Laterally, the jugal does not reach the quadrate but leaves the quadratojugal visible.

The quadratojugal is very fragmentary and can only be observed from the right side. The preserved part is reduced to a lamina between the quadrate and jugal, where it is sculptured and appears on the lateral side. It does not send any process along the lower temporal bar.

Both quadrate bones are preserved, but the right one is in a better state of preservation. Due to fractures and deformation, the quadrate rami are almost vertically oriented. Despite such unnatural verticalization, the quadrate rami are unusually elongate and are as long as the descending squamosal prongs. As a comparison, the quadrate rami are shorter than the squamosal prongs in *Crocodylus* or *Caiman*. The medial quadrate hemicondyle is smaller than the massive lateral hemicondyle. The foramen aëreum appears on the dorsomedial margin of the quadrate.

The left postorbital is preserved. Its lateral margin is convex and gives to the anterior skull table a gently continuous shape. The postorbital bar is mediolaterally compressed and is therefore expanded anteroposteriorly.

The squamosal is best preserved on the right side. Here, a prominent prong is visible. This prong projects far posteriorly behind the level of the occipital condyle and beyond the lateral margin of the skull table. The squamosal extends far ventrally on the paroccipital process. Its suture with the quadrate lies on the ventral margin of the otic notch. The dorsal margin of the otic notch is not straight but bowed. The squamosal extensively overhangs the occipital region.

The supraoccipital participation to the posterior portion of the skull table is limited to a small incursion in dorsal aspect. The supraoccipital is, however, massive and extensively overhangs the occiput. A strong median crest projects ventrally and is framed by two massive spines that project posteriorly beyond the posterior margin of the skull table. A pair of grooves delimits the spines from the median crest.

The exoccipital is severely fractured but is nevertheless almost complete on the right side. It covers most of the occipital portion of the skull, forming all the margin of the foramen magnum. It laterally expands and creates a

developed process overhanging the cranioquadrate passage. However, the passage, while delimited by a depression, is not well preserved. A large foramen vagus pierces the bone at the level of the foramen magnum. The ventral process of the exoccipital projects beyond the foramen caroticum posterius but does not attain the ventralmost level of the basioccipital.

The basioccipital is divided into two regions. First, the occipital condyle presents a foramen in its dorsal part. Second, the vertical basioccipital plate presents two shallow pillars, then a strong descending single pillar in its ventralmost portion. The basioccipital plate is very long in proportion compared to that of extant *Crocodylus* or *Alligatoridae*.

The basisphenoid is incomplete but its suture can be observed at the base of the basioccipital plate. It forms the posterior margin of the large median Eustachian opening.

The foramen ovale is large and its organization shows that the prootic is well visible inside this foramen for the entire posterior margin. It is not obscured by any other bones but does not participate in the wall. The suture between quadrate and pterygoid is not obvious but may have been straight from the foramen ovale to the posterior margin of the braincase. The laterosphenoid is heavily fragmented but it is recognizable as forming the anterodorsal portion of this foramen.

The pterygoid wings appear vertical, but it is impossible to assess the contribution of deformation. The *Torus transiliens* is thick and finely pitted. It corresponds to the attachment of tendons for the M. pterygoideus posterior. The posterior margin of the wing is uneven and slightly concave on its lateral side. Medially, the pterygoid is notched at the level of the median Eustachian passage. The lateral walls of this notch send two processes posteriorly. The choanae are large and square. Their posterior margin is almost continuous with the pterygoid surface. They are slightly more elongate in the anteroposterior direction. They pierce the pterygoids near their posterior margin and face anteroventrally. A lamina divides the choanae and enters the dorsal wall of the cavity. The pterygoid forms the posterior margin of the suborbital fenestra and is wide there. It is slightly notched at this level.

The ectopterygoid sends a posterior process onto the pterygoid wing but does not reach its posteriormost margin. The suture with the pterygoid is almost straight. Dorsally, the posterior process of the ectopterygoid on the jugal is almost absent. The anterior process, however, projects far along the tooth row and is contiguous with the last five alveoli and contributes directly to the last alveolus.

The palatine is a long bone that participates in the medial margin of the suborbital fenestra. The right side is preserved in its entirety for the ventral part. It is anteroposteriorly straight and its lateral wall is vertical in its posterior portion. The suture with the pterygoid occurs at the posteriormost level of the suborbital fenestra. Near the anterior level of the fenestra, the suture with the maxilla shows a mediolateral direction. A small foramen pierces the bone near the median suture. More anteriorly, the palatine penetrates into the maxilla by sending a long and slender pointed process reaching the level of the seventh maxillary alveolus.

The mandible is very fragmentary. Pieces of both dentary bones are present and indicate the presence of at least twelve alveoli in the left bone. The right dentary is broken at the level of the possibly confluent and largest alveoli, as evidenced by the size of their remaining wall. At least eleven alveoli can be counted in this bone, therefore providing an estimate of at least fifteen alveoli in this ramus. Numerous foramina pierce the base of the alveoli. The splenial is not preserved but its suture on the dentary indicates that it was excluded from the symphysis. The profile of the tooth row is slightly constricted

Table 1. Character codings for *Diplocynodon elavericus*

5	10	15	20	25	30	35	40	45	50	55	60	65	70	75
?????	?????	?????	?????	?????	?????	?????	0????	??10?	??11?	??0??	????1	??1??	??0?1	1100?
80	85	90	95	100	105	110	115	120	125	130	135	140	145	150
?1110	00110	?0130	00?0?	?0?0	?1001	??001	00???	0?1??	?1110	011??	210?1	????1	0??0?	??111
155	160	165	167											
110??	?????	????1	12											

Key to characters in Brochu (1999, 2004).

behind the fifth alveolus with the presence of small alveoli. Alveoli then become larger and the profile becomes elevated from the ninth or tenth alveolus. The surangular consists of a fragment from the right posterodorsal portion. The smooth attachment for *M. adductor mandibulae superficialis* and *medius* is large and inclined laterally. A small fossa is present lateral to the dorsal contribution of the surangular to the articular jaw joint. The corresponding articular consists of the articular capsule as well as the descending anterior process. The surangular–articular suture is simple, but due to preservation, it is not possible to properly assess the position of the visible foramen relative to the suture. There is no sulcus between the articular and surangular. The foramen aëreum is visible and is laterally shifted.

The dentition of this taxon consists of conical teeth in the premaxilla and in most of the maxilla. From the eleventh alveolus, the teeth are slightly mediolaterally compressed and blunter. Two ridges run from the mesial face to the apex. The enamel is smooth.

Postcranial elements are represented by a few osteoderms from the dorsal shield. The best preserved of all is rectangular and presents large and shallow rounded pits on its dorsal surface. A shallow median ridge is present and runs along most of its length, except anteriorly where the smooth articulation facet is present. This ridge slightly overhangs the posterior margin. Laterally and medially, the osteoderm is sutured. Its ventral surface is smooth with criss-crossing striation for epaxial muscle insertion.

5. Comparison with other species of the genus

The quadrate rami are longer than in any other species of *Diplocynodon* or alligatoroids. Discarding deformation, the quadrate rami would have projected well beyond the posterior margin of the skull table, whereas among other species of *Diplocynodon*, the quadrate rami are located close to the level of the posterior skull table margin, when observation is made from a dorsal point of view. In contrast to *D. darwini*, *D. ratelii*, *D. muelleri*, *D. tormis*, *D. hantoniensis* or *D. styriacus*, the palatine–pterygoid suture is located at the posterior level of the suborbital fenestra in *D. elavericus*.

Diplocynodon elavericus is younger than *Diplocynodon hantoniensis* from the Headon Hill formation (Early Priabonian: Hooker, Cook & Benton, 2005) of the United Kingdom. These two species are very similar in general aspect. They both show a broad and stout rostrum, well-developed squamosal prongs that project far posteriorly, well-developed supraoccipital spines projecting posteriorly, the absence of a preorbital ridge and comparable head size and proportions (see Table 2 for comparison). However, a number of differences

Table 2. Comparative measurements (in mm) of the skull of *Diplocynodon elavericus* (Rhinopolis B3) and *Diplocynodon hantoniensis*

Characteristics	Rhinopolis B3	BMNH 30393
Length of skull from tip of snout to posterior edge of cranial table	~ 345	490
Maximal width of skull, across quadratojugals	206	323
Length of snout	~ 190	289
Length of post-snout region, from anterior border of orbit to posterior edge of cranial table	~ 155	201
Maximal width of snout	128	163
Maximal length of orbit	~ 66	72
Maximal width of orbit	43	50
Interorbital width	19	36
Length of cranial table, through centre of supratemporal fenestrae	82	124
Width of cranial table, across centres of supratemporal fenestrae	105	148
Maximal length of supratemporal fenestra	39	56
Maximal width of supratemporal fenestra	26	40
Interfenestral width	17	14
Length of incisive foramen	<21	20
Length of long axis of suborbital fenestra	92	149
Length of short axis of suborbital fenestra	47	59
Interfenestral width of palatines	18	28
Width of choanae	23	29
Width across pterygoid flanges	137	299

are to be observed, including the completely flat dorsal surface of the parietal in *D. elavericus*. *D. elavericus* and *D. hantoniensis* are among the largest known species of the genus. Such a concave parietal can be observed in *D. hantoniensis*, as well as in *D. cf. hantoniensis* from the Oligocene of Dordogne (Vignaud *et al.* 1996). Other differences include the presence of an elevated rim on the medial margin of the supratemporal fenestrae in *D. hantoniensis*. Also, the shape of the palatine projection within the maxilla is different. In *D. hantoniensis*, the anterior palatine projection is wide and squared off and reaches the level of the ninth maxillary alveolus. In *D. elavericus*, the palatine projection is slender and pointed and reaches further anteriorly between the level of the sixth and seventh alveoli.

Diplocynodon tormis from the Late Eocene of Salamanca, Spain, is older than *Diplocynodon elavericus*

and *Diplocynodon hantoniensis* as it is Bartonian in age (Buscalioni, Sanz & Lourdes, 1992). It is, however, very different in size and skull proportions, and the differences exhibited render it less comparable to *D. elavericus* than *D. hantoniensis*. The basalmost member of Diplocynodontidae, *D. darwini*, has a relatively short rostrum together with *D. muelleri*, while *D. ratelii*, *D. gervaisi* and specimens referred to *D. styriacus* show the most slender morphology. The current interrelationship hypothesis proposed here reveals that the general skull proportions do not have any phylogenetic meaning, *D. elavericus* and *D. hantoniensis* not being closely related to each other. Their contemporaneous occurrence shows that several lineages inhabited Europe with probably similar ecologies or feeding habits. This could explain such morphological convergence despite their different phylogenetic positions.

Vignaud *et al.* (1996) recognized that the posterior region of the maxillary tooth row is mesially bound by the ectopterygoid in *D. ratelii*, *D. gervaisi* and *D. tormis* but not in *D. hantoniensis*. I disagree, however, about the condition in *D. hantoniensis*, and the preceding description shows that the same is true for *D. elavericus*. Such a character might be added to the generic diagnosis of *Diplocynodon* pending observations on other species. Piras & Buscalioni (2006) described the maxilla of *D. muelleri* as sending an outgrowth between the tooth row and the ectopterygoid. In *D. tormis* (Buscalioni, Sanz & Lourdes, 1992), the ectopterygoid is described as running beside the alveolar border; however, the interpretive drawing seems to indicate otherwise. In specimens attributed to *D. styriacus* (Ginsburg & Bulot, 1997), there is no outgrowth of the maxilla separating tooth row from ectopterygoid in the photos of the authors (fig. 2, p. 115; fig. 3, p. 118), although their drawings indicate otherwise.

6. Phylogenetic analysis

In order to compute a maximum of alligatoroid taxa, *Diplocynodon elavericus* was coded (Table 1) and included in the matrix of Brochu (1999, 2004), together with the recently coded *Diplocynodon muelleri* and *Diplocynodon tormis* by Piras & Buscalioni (2006). Nine other taxa were taken from the matrix of Salisbury *et al.* (2006), and their codings were adjusted to the present matrix. Because it has been demonstrated that *Borealosuchus* was different from the alligatoroid *Leidyosuchus* (Brochu, 1997), four taxa of the genus *Borealosuchus* were included in the analysis (*B. sternbergii*, *B. acutidentatus*, *B. wilsoni* and *B. formidabilis*) to test its monophyly. Two gavialoids (*Gavialis gangeticus* and *Thoracosaurus macrorhynchus*), as well as two other crocodyloids (*Prodiplocynodon langi* and '*Crocodylus*' *affinis*'), were added to the analysis and permitted wide sampling of the Eusuchia. The basal eusuchian *Hylaeochampsa vectiana* was defined as the outgroup taxon. A total of 49 ingroup taxa were treated under multiple heuristic

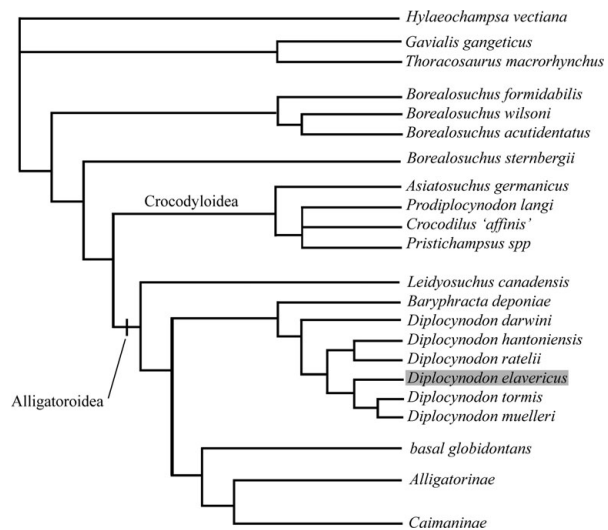


Figure 10. Hypotheses of relationships for *Diplocynodon elavericus* included in the matrix of Brochu (1999, 2004) with a total number of seven diplocynodontids. Relationships with more derived members of Alligatoroidea were simplified for clarity of reading but the results do not differ from that of Brochu (1999, 2004).

searches with Paup* (Swofford, 2002) for 100 random-seed replicates. The analysis yielded 2432 equally most-parsimonious trees with a length of 397 steps (CI, excluding uninformative characters = 0.4557; RI = 0.7721).

The topology of the strict consensus tree (Fig. 10) is mostly consistent with the results of Salisbury *et al.* (2006), with Alligatoroidea and Crocodyloidea being sister clades, although *Pristichampsus* spp. is presently incorporated in a polytomy with *Prodiplocynodon langi* and '*Crocodylus*' *affinis*', whereas it is basal to the Brevirostres in the results of Salisbury *et al.* (2006). Also here, *Borealosuchus* is not monophyletic: *B. sternbergii* sits in a more derived position than the clade composed of the three other species of *Borealosuchus*. The limited resolution at the base of Eusuchia can be interpreted as a result of the small taxon sampling in the analysis and may also explain why Gavialoidea is not sister-group to *Borealosuchus* but forms a polytomy with *Hylaeochampsa vectiana*. However, the purpose of this sampling was to polarize characters in order to stabilize the relationship within Alligatoroidea. The topology of this clade is consistent with the results of Brochu (1999, 2004) and is also consistent with the results of Piras & Buscalioni (2006) in the basal arrangement of the Diplocynodontidae with *Baryphracta deponiae* as the basalmost member, and then *D. darwini* as the basalmost diplocynodontine. Moreover, the internal nodes are here better resolved; *D. hantoniensis* and *D. ratelii* are sister taxa and form the sister group to the three remaining taxa: *D. elavericus* is the sister taxon to *D. muelleri* and *D. tormis*, which form a clade. A Bremer decay analysis tested the robustness of the arrangement; one step longer than the optimal tree length did not alter the major divisions. Internal relationships are polytomic, but *Leidyosuchus*

canadensis, Diplocynodontidae, basal globodontans, Alligatorinae and Caimaninae are well defined.

Diplocynodontidae are supported by the presence of paired osteoderms that suture together (39–2) and a linear frontoparietal suture (86–1), although these traits are unknown in *D. elavericus*. Also unknown in *D. elavericus*, the nasal excluded from the external naris (95–2) as well as the foramen opening on the angular–surangular suture, are still considered ambiguous because they are also present in *Borealosuchus* (Brochu, 1999). The linear quadrate–pterygoid suture from the basisphenoid to the exposure of the foramen ovale (127–1) remains ambiguous as it is originally only observed in *D. ratelii* (Brochu, 1999) but is now found in *D. elavericus*. The phylogenetic results unambiguously present the splenial as excluded from the symphysis as a synapomorphy for Diplocynodontinae (43–1), and this is again confirmed here with *D. elavericus*. The presence of confluent dentary teeth of similar size (3+4) in *D. elavericus* remains ambiguous as it is also shared with *Leidyosuchus canadensis*, *Borealosuchus* and also *Deinosuchus* (Brochu, 1999). Piras & Buscalioni (2006) defined the genus *Diplocynodon* as possessing a large medial jugal foramen (120–1), but this trait is coded as small for *D. darwini* (Brochu, 1999) and is unknown in *D. elavericus*. Piras & Buscalioni (2006) also include in this definition the trait ‘largest dentary alveolus immediately caudal to fourth is 10, 11 or 12 (167–2)’, which is consistent with observations made on *D. elavericus*.

The fragmentary nature of *D. elavericus* does not help to define further characters for the genus *Diplocynodon*. Nevertheless, its inclusion triggers a resolution within Diplocynodontidae. This arrangement does not show a continuous succession of species through time. Instead, old records show more affinities with recent ones, as exemplified by sister taxa such as *D. tormis* + *D. muelleri*, or *D. hantoniensis* + *D. ratelii*. This topology remains tentative. Indeed, the Bremer decay analysis demonstrated a weak support and it might be preferable to include more complete taxa that would bring more robustness into the internal relationship of the Diplocynodontidae. Interestingly, the sister group relationship of *D. hantoniensis* implies a long fossil record for *D. ratelii* from the Late Eocene up to the Early Miocene. For this reason, it might be worth testing the relationship of the specimen from the Early Oligocene of Céreste, attributed to *D. ratelii* (Brinkmann & Rauhe, 1998). Finally, the most reliable aspect of the inclusion of *D. elavericus* in a phylogenetic framework permits confirmation of the monophyly of the Diplocynodontidae as well as the endemic nature of this clade to Europe.

7. *Diplocynodon* in the context of the Late Eocene climate change

The Palaeogene and Neogene fossil record of crocodylians in Europe is not continuous, but a broad pattern of faunal succession has been identified.

Buffetaut (1982) gave a first brief review in which he emphasized a decline in diversity during the Eocene period. A similar pattern can be observed when looking at the Eocene–Oligocene fossil record of the Duero Basin, Spain (Martín de Jesús *et al.* 1987), or that of Italian crocodylians as listed by Kotsakis, Delfino & Piras (2004). Despite these observations, European crocodylians have received little attention in this respect. In his review of crocodylian diversity from the Cretaceous to the present, Markwick (1998a) identified such a diversity decline during the Late Eocene over a global scale and invoked the influence of climate variation on crocodylian diversity. However, he pointed out that a sampling effect could influence such results. Due to the incompleteness of the fossil record, it is challenging to link patterns of faunal turnover with the evolution of climatic conditions. Although this problem is inherent to the fossil record of vertebrates, sparse but well-dated occurrences can provide important pieces of evidence, especially because semi-aquatic crocodylians are ectothermic and thus are dependent on environmental conditions (Berg, 1965; Hutchison, 1982; Antunes, 1994; Markwick, 1998a). Therefore, their occurrence implies sub-tropical or tropical conditions. *Diplocynodon elavericus* is Middle Priabonian in age and represents one of the youngest known records of crocodylians in the Eocene period of Europe (Fig. 11). Of similar age, isolated teeth and osteoderms have been attributed to *Diplocynodon* from the Priabonian of the Basque country, Spain (Astibia *et al.* 2000). Nevertheless, *Diplocynodon elavericus* is recovered at a higher latitude than the Spanish remains and introduces the discussion about the evolution of the genus in the temperature decline of the Late Eocene.

Evolution of global temperatures through the Cenozoic has received particular attention during the last decade thanks to quantitative analyses. Isotopic composition of benthic foraminifera (Zachos *et al.* 2001) and biomarkers (Schouten *et al.* 2008) revealed a negative shift in global temperature at the Eocene–Oligocene transition, a climatic phenomenon that was previously hypothesized to account for turnover in mammalian communities of Europe and known as ‘La Grande Coupure’ (Stehlin, 1910; Legendre, 1989 for a review; Hooker, Collison & Sille, 2004). This climatic transition marks the end of a greenhouse world, which peaked in temperature after the Palaeocene–Eocene boundary. During most of the Eocene period, continental mean annual air temperature seems to have been relatively constant (Mosbrugger, Utescher & Dilcher, 2005; Schouten *et al.* 2008), with progressively increasing seasonality from the end of the Middle Eocene, as revealed by floras from Central Europe (Mosbrugger, Utescher & Dilcher, 2005). However, the present resolution of the climatic record is not sufficient to allow a precise climatic reconstruction, and although it has become widely admitted that a permanent ice sheet settled on Antarctica from the earliest Oligocene (Miller, Wright & Fairbanks, 1991; Lear, Elderfield & Wilson, 2000; Zachos *et al.* 2001;

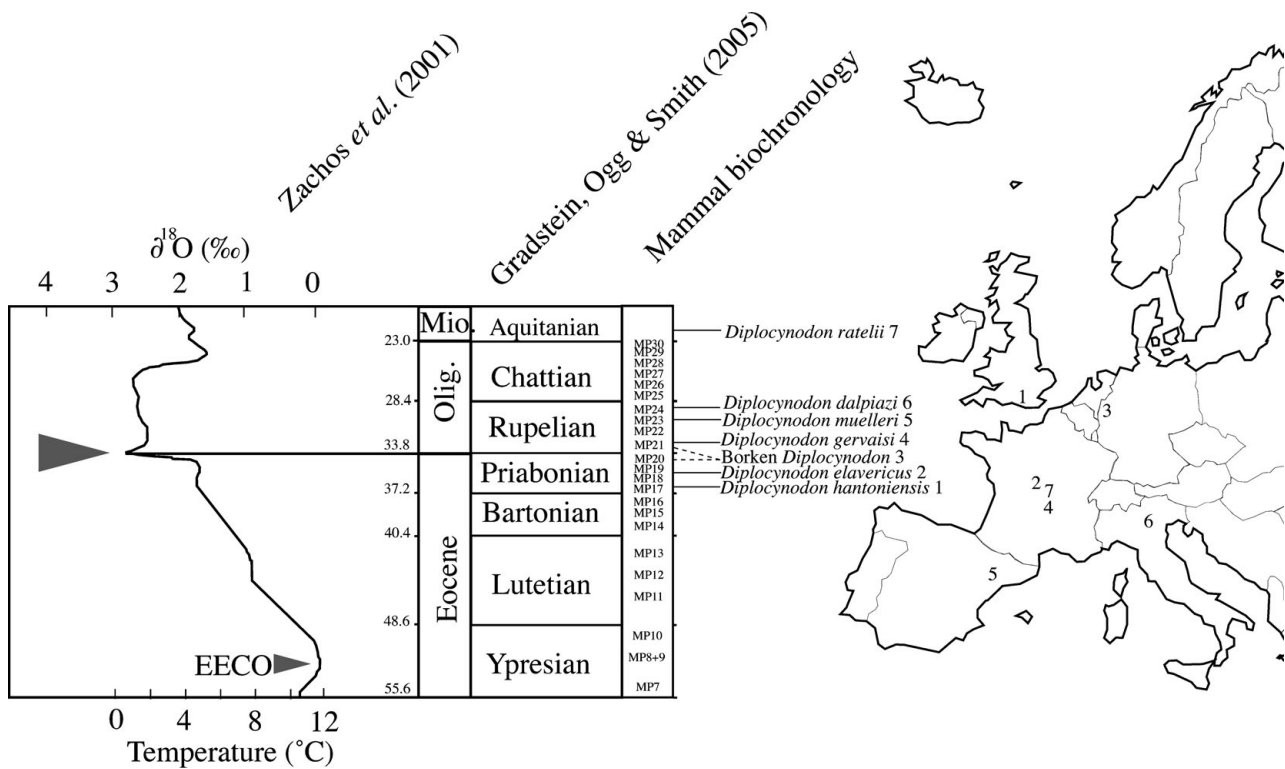


Figure 11. Geographic occurrences of six *Diplocynodon* species compared to their stratigraphic position (numerical ages according to Gradstein, Ogg & Smith, 2005, and European Land Mammal Ages according to BiochroM, 1997) and the global temperature curve across the Late Eocene and Oligocene (after Zachos *et al.* 2001). Numbers refer to the localities around the Eocene–Oligocene boundary having yielded *Diplocynodon*: 1 – Hordwell; 2 – Domérat; 3 – Borken; 4 – Ronzon; 5 – Lleida; 6 – Monteviale; 7 – St-Gérard-le-Puy. EECO – Early Eocene Climatic Optimum. Note the unsettled stratigraphic position of the remains from Borken as highlighted by the dashed line.

Coxall *et al.* 2005; Ivany *et al.* 2006), there is some evidence, including reports of ice-rafted debris, to suggest that a continental ice sheet and glaciers were already present in the northern hemisphere as early as the Middle Eocene (Moran *et al.* 2006; Eldrett *et al.* 2007; Tripatti *et al.* 2008). Such climatic evolution must have had an influence, for example, on the distribution of ectothermic vertebrates.

Late Eocene and Oligocene continental crocodylian faunas consist of only a single taxon at any given locality. This contrasts significantly with Early or Middle Eocene ecosystems, in which niche partitioning allowed several taxa to co-occur. For example, the Lutetian localities of Messel or Monte Bolca include terrestrial taxa such as the ziphodont *Pristichampsus*, the blunt-snouted ‘*Allognathosuchus*’, as well as semi-aquatic forms such as *Asiatosuchus*-like taxa (*sensu* Delfino & Smith, 2009), or *Diplocynodon* (Berg, 1966; Kotsakis, Delfino & Piras, 2004). A bias in sampling cannot be excluded for younger faunas as they are not preserved as Lagerstätten, as is the case at Messel or Monte Bolca. However, from the Priabonian onward, ziphodont crocodylians are no longer found, whereas their remains are not so rare in Lutetian or Bartonian fluvial deposits, their youngest European occurrence being from the Bartonian (MP16, BiochroM, 1997) of La Badayré/Sables du Castrais (Berg, 1966) and a single tooth from the Quercy (imprecise date–

Bartonian after Buffetaut, 1982). The last record of *Asiatosuchus*-like taxa is from the Bartonian of Camburg, Germany (Vasse, 1992). The latest basal alligatorine from Europe is *Arambourgia gaudryi* from Quercy and may represent an exception as it is as old as or slightly older than the new taxon from Domérat (MP18 or MP19) (Rage, 2006). While semi-aquatic fossil crocodylians were certainly ectothermic, as this represents a great advantage in such environment (Seymour *et al.* 2004 for a review), terrestrial crocodylians may have had a different metabolic regime and thus, their climatic requirements may have differed from that of semi-aquatic crocodylians. Extant crocodylians live in a specific temperature window and any variation outside of it has consequences for their life (Lang, 1979; Markwick, 1998b): either they are pushed to migrate or they eventually die. It is, however, impossible to quantify the range of temperatures that the extinct crocodylians could have sustained, and thus comparison with the known increasing seasonality in continental ecosystems of Europe is limited. It is clear, however, that the Eocene–Oligocene negative temperature shift post-dates the crocodylian diversity decline and cannot be considered as a possible cause.

As was proposed by Buffetaut (1982), progressive temperature decline from the middle Late Eocene may have entered the range in which most crocodylian taxa could no longer survive. In this light, the latitudinal

distribution of the genus *Diplocynodon* through time is interesting (Fig. 11). *Diplocynodon hantoniensis* is recorded from the base of the Priabonian stage in southern England. *Diplocynodon elavericus* is recorded at a more southern latitude in France later on (MP18–20). In any case, these occurrences are recorded prior to the negative temperature shift of the Eocene–Oligocene boundary, which is considered to take place at the limit between the mammal zones MP20 and MP21 (Escarguel, Marandat & Legendre, 1997; but see Hooker, Collinson & Sille, 2004). Subsequent to the dramatic drops in temperatures, the next record of *Diplocynodon* is that from Ronzon (Berg, 1966), which is dated as basal Rupelian (MP21) and contains *Diplocynodon gervaisi* basking in sub-tropical to tropical conditions. Another lower Oligocene (Rupelian, MP24) French locality near Céreste produced a specimen attributed to *Diplocynodon ratelii* (Brinkmann & Rauhe, 1998). It is more or less of the same age as *Diplocynodon dalpiazii* from Monteviale, Italy (Del Favero, 1999). Indeed, it cannot be ruled out that *Diplocynodon* suffered from temperature decline during ‘La Grande Coupure’ and that low latitude regions of Europe may have constituted climatic refugia before recolonization of Europe became possible during the following Oligocene warming, with *D. gervaisi* as an example. A progressive southward migration of *Diplocynodon* during this climatic deterioration would represent a tempting explanation, nevertheless the continental record is not continuous and the absence of crocodylians at higher latitude localities of Europe needs to be tested, especially near the Eocene–Oligocene boundary. In this regard, a mandibular fragment was reported from the Melanienton formation at Borcken, northern Germany (Gramann, 1958). This formation is currently attributed a Late Eocene age on the basis of mammals (MP20; Biochrom, 1997), but the locality of Borcken has never yielded any mammals and was usually considered Early Oligocene in age (Gramann, 1958). Recent calibration using nannoplankton places the Melanienton formation across the Eocene–Oligocene boundary (Martini & Reichenbacher, 2007). As no information was provided concerning the position of the specimens from Borcken within the formation, the *Diplocynodon* remains from that locality could be either Late Eocene or Early Oligocene. A southward shift in relation to climatic deterioration has already been proposed for *Diplocynodon* during the Miocene (Böhme, 2003) and a similar shift in distribution may well have taken place at the Eocene–Oligocene transition when temperatures dropped more rapidly than during the gradual Late Miocene cooling. However, two hypotheses remain to be tested. *Diplocynodon* may have been able to endure several months below 0 °C, as is the case for the extant *Alligator sinensis*. Such an ability might have helped it to survive the Eocene–Oligocene climatic deterioration and would explain the success of *Diplocynodon* in continental ecosystems of Europe over other crocodylian taxa. While Markwick (1998b) presented all extant crocodylians as having similar thermal preferences,

Lang (1979) measured differences of body temperature between *Alligator mississippiensis* and *Crocodylus acutus*, and suggested these might reflect different thermoregulatory strategies. That extant *Alligator* is more cold-tolerant than extant *Crocodylus* still requires a quantitative assessment. Although cold-tolerance in *Diplocynodon* has to be tested isotopically (oxygen from enamel apatite), it may extend the optimization of this character from Alligatoridae (Alligatorinae + Caimaninae) down to basal Alligatoroidea. A second option, which does not exclude the former, is a possible southward migration of *Diplocynodon* during the Late Eocene period. Isolation of populations by climatic barriers would have promoted speciation within this genus. Coeval localities are not abundant, but the recognized high diversity of *Diplocynodon* species might be the result of such speciation mechanisms. A comprehensive review of the relationships of all the known *Diplocynodon* species is pending and may provide an interesting comparative basis for the reconstruction of possible migratory events.

8. Conclusions

Relatively complete remains of a new *Diplocynodon* taxon allow comparison with other members of the genus. *Diplocynodon elavericus* is more closely related to the Spanish *Diplocynodon* (*D. muelleri* and *D. tormis*) than to *Diplocynodon hantoniensis* or *Diplocynodon ratelii* from more northern localities of Europe. The new taxon adds to the diversity of this successful group in continental ecosystems of Europe. It is widely recognized that a global climatic event led to a decrease in temperatures near the Eocene–Oligocene boundary. Biotic evidence, including the evolution of crocodylian assemblages, has the potential to provide reliable proxies insofar as it may record such a climatic deterioration, namely by presenting a diversity decline. At that time, the presence of continental ice in the northern hemisphere is consistent with such a hypothesis. In any case, the extensive fossil record of *Diplocynodon* in Europe throughout the Palaeogene and early Neogene might be an indirect evidence for the ability of this genus to sustain low temperatures.

Acknowledgements. The author expresses his gratitude to E. Buffetaut for discussion and advice during the completion of this work. S. Jouve and one anonymous reviewer significantly helped to improve the content of the manuscript. Former labmates K. Travouillon and G. Suan, as well as doctoral students in geology, Lyon 1, provided entertaining support during the long preparation of the specimen. F. Escuillié brought the present specimen to my attention. S. Hervet provided much help in making the specimen accessible from the Association Rhinopolis. The author was funded by *Le Conseil Général de l’Allier*.

References

- ANTUNES, M. T. 1994. On Western Europe Miocene gavials (Crocodylia): their paleogeography, migrations

- and climatic significance. *Comunicações do Instituto Geológico e Mineiro* **80**, 57–69.
- ASTIBIA, H., ARANBURU, A., Pereda SUBERBIOLA, X., MURELAGA, X., SESÉ, C., CUESTA, M. A., MOYA-SOLA, S., BACETA, J. I., BADIOLA, A. & KÖHLER, M. 2000. Un nouveau site à vertébrés continentaux de l'Éocène supérieur de Zambrana (Bassin de Miranda-Treviño, Alava, Pays Basque). *Géobios* **32**, 233–48.
- BERG, D. E. 1965. Krokodile als Klimazeugen. *Geologische Rundschau* **54**, 328–33.
- BERG, D. E. 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*?, aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **52**, 1–105.
- Biochrom'97. 1997. Synthèses et tableaux de corrélations. In *Actes du Congrès Biochrom'97* (eds J.-P. Aguilar, S. Legendre & J. Michaux), pp. 769–805. Mémoires et Travaux de l'E. P. H. E. Inst. Montpellier.
- BÖHME, M. 2003. The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* **195**, 389–401.
- BRAVARD, A. 1843. Considérations sur la distribution des mammifères terrestres fossiles dans le département du Puy-de-Dôme. *Annales scientifiques, littéraires et industrielles de l'Auvergne* **16**, 1–439.
- BRINKMANN, W. & RAUHE, M. 1998. *Diplocynodon ratelii* Pomel, 1847 (Crocodylia, Leidyosuchidae) aus dem Unter-Oligozän von Céreste (Südfrankreich). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **209**, 295–321.
- BROCHU, C. A. 1997. A review of "Leidyosuchus" (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *Journal of Vertebrate Paleontology* **17**, 679–97.
- BROCHU, C. A. 1999. Phylogeny, systematics, and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology Memoir* **6**, 9–100.
- BROCHU, C. A. 2004. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *Journal of Vertebrate Paleontology* **24**, 857–73.
- BUFFETAUT, E. 1982. Les crocodiliens Européens et la coupure Eocene–Oligocene. *9ème réunion annuelle des sciences de la terre, Paris. Société Géologique de France*.
- BUSCALIONI, A. D., SANZ, J. L. & LOURDES, M. C. 1992. A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *Neues Jahrbuch für Geologie und Paläontologie* **187**, 1–29.
- COXALL, H. K., WILSON, P. A., PALIKE, H., LEAR, C. H. & BACKMAN, J. 2005. Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. *Nature* **433**, 53–7.
- DEL FAVERO, L. 1999. Un esemplare di *Diplocynodon* Pomel, 1847 (Crocodylia, Leidyosuchidae) conservato nel museo geopaleontologico dell' Università di Padova. *Lavori Società Veneta di Scienze Naturali* **24**, 107–17.
- DELFINO, M. & SMITH, T. 2009. A reassessment of the morphology and taxonomic status of 'Crocodylus' *depressifrons* Blainville, 1855 (Crocodylia, Crocodyloidea) based on the Early Eocene remains from Belgium. *Zoological Journal of the Linnean Society* **156**, 140–67.
- EFIMOV, M. B. 1988. The fossil crocodiles and champsosaurides of Mongolia and USSR. *Transactions, the joint Soviet–Mongolian paleontological expedition* **36**, 1–108.
- ELDRETT, J. S., HARDING, I. C., WILSON, P. A., BUTLER, E. & ROBERTS, A. P. 2007. Continental ice in Greenland during the Eocene and Oligocene. *Nature* **446**, 176–9.
- ESCARGUEL, G., MARANDAT, B. & LEGENDRE, S. 1997. Sur l'âge numérique des faunes de mammifères du paléogène d'Europe occidentale, en particulier celles de l'éocène inférieur et moyen. In *Actes du Congrès Biochrom'97* (eds J.-P. Aguilar, S. Legendre & J. Michaux), pp. 769–805. Mémoires et Travaux de l'E. P. H. E. Inst. Montpellier.
- GINSBURG, L. & BULOT, C. 1997. Les *Diplocynodon* (Reptilia, Crocodylia) de l'Orléanien (Miocène inférieur à moyen) de France. *Geodiversitas* **19**, 107–28.
- GMELIN, J. F. 1789. *Linnei Systema Naturae*. Leipzig: G. E. Beer.
- GRADSTEIN, F. M., OGG, J. G. & SMITH, A. G. 2005. *A geologic time scale 2004*. Cambridge: University Press Cambridge, 589 pp.
- GRAMANN, F. 1958. Der Crocodilide *Diplocynodon hantoniensis* (Wodd) aus dem unteroligozänen Melaninton Niederhessens. *Notizblatt Hessischen Landesamtes Bodenforschung* **86**, 77–8.
- GRANDSTAFF, B. S., PARRIS, D. C., DENTON, R. K. & GALLAGHER, W. B. 1992. *Alphadon* (Marsupialia) and *Multituberculata* (Allotheria) in the Cretaceous of eastern North America. *Journal of Vertebrate Paleontology* **12**, 217–22.
- GRAY, J. E. 1844. *Catalogue of tortoises, crocodilians, and amphisbaenians in the collection of the British Museum*. British Museum (Natural History), London, 80 pp.
- GUANBANG, L. & GUIKUN, C. 1993. Late Cenozoic Crocodylia fossils from Jiangsu. *Vertebrata Palasiatica* **31**, 61–4.
- HOOKE, J. J., COLLINSON, M. E. & SILLE, N. P. 2004. Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event. *Journal of the Geological Society, London* **161**, 161–72.
- HOOKE, J. J., COOK, E. & BENTON, M. J. 2005. British Tertiary fossil mammal GCR sites. In *Mesozoic and Tertiary Fossil Mammals and Birds of Great Britain* (eds M. J. Benton, E. Cook & J. J. Hooker), pp. 67–124. Geological Conservation Review Series no. 32, JNCC, Peterborough.
- HUA, S. 2004. Les crocodiliens du Sparnacien (Eocène inférieur) du Quesnoy (Oise, France). *Oryctos* **5**, 57–62.
- HUTCHISON, J. H. 1982. Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the North-Central region of Western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* **37**, 149–64.
- HUXLEY, T. H. 1875. On *Stagonolepis Robertsoni*, and on the evolution of the Crocodylia. *Quarterly Journal of the Geological Society of London* **3**, 423–38.
- IORDANSKY, N. N. 1973. The skull of the Crocodylia. In *Biology of the Reptilia, Vol. 1, Morphology* (eds C. Gans & T. S. Parson), pp. 201–62. London and New York: Academic Press.
- IVANY, L. C., VAN SIMAEYS, S., DOMACK, E. W. & SAMSON, S. D. 2006. Evidence for an earliest Oligocene ice sheet on the Antarctic Peninsula. *Geology* **34**, 377–80.
- KOTSAKIS, T., DELFINO, M. & PIRAS, P. 2004. Italian Cenozoic crocodilians: taxa, timing and palaeobiogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **210**, 67–87.
- LANG, J. W. 1979. Thermophilic response of the American Alligator and the American Crocodile to feeding. *Copeia* **1**, 48–59.

- LEAR, C. H., ELDERFIELD, H. & WILSON, P. A. 2000. Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca benthic foraminiferal calcite. *Science* **287**, 269–72.
- LEGENDRE, S. 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. *Münchner Geowissenschaftliche Abhandlungen A* **16**, 1–110.
- MARKWICK, P. J. 1998a. Crocodylian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology* **24**, 470–97.
- MARKWICK, P. J. 1998b. Fossil crocodylians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* **137**, 205–71.
- MARTIN, J. E. & BENTON, M. J. 2008. Crown clades in vertebrate nomenclature: correcting the definition of Crocodylia. *Systematic Biology* **57**, 173–81.
- MARTÍN DE JESÚS, S., JIMENEZ FUENTES, E., FINCIAS, B., DEL PRADO, J. M. & MULAS ALONSO, E. 1987. Los Crocodylia del Eoceno y Oligoceno de la Cuenca del Duero. Dientes y osteodermos. *Revista Española de Paleontología* **2**, 95–108.
- MARTINI, E. & REICHENBACHER, B. 2007. Nannoplankton und fisch-otolithen in den Mittleren Pechelbronn-Schichten (Unter-Oligozän, Oberrheingraben/Mainzer Becken). *Geologische Abhandlungen Hessen* **116**, 235–73.
- MELOUX, J. L., REMY, J. A., SUDRE, J., TURLAND, M. & VIANEY-LIAUD, M. 1996. Découverte d'une faune à *Palaeotherium* et *Anoplotherium* dans le bassin tertiaire de Domérat (Allier). *Géologie de la France* **2**, 69–78.
- MILLER, K. G., WRIGHT, J. D. & FAIRBANKS, R. G. 1991. Unlocking the ice house: Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion. *Journal of Geophysical Research* **96**, 6829–48.
- MOOK, C. C. 1960. *Diplocynodon* remains from the Bridger Beds of Wyoming. *American Museum Novitates* **2007**, 1–4.
- MORAN, K., BACKMAN, J., BRINKHUIS, H., CLEMENS, S. C., CRONIN, T., DICKENS, G. R., EYNAUD, F., GATTACCECA, J., JAKOBSSON, M., JORDAN, R. W., KAMINSKI, M., KING, J., KOC, N., KRYLOV, A., MARTINEZ, N., MATTHIESSEN, J., MCINROY, D., MOORE, T. C., ONODERA, J., O'REGAN, M., PÄLIKE, H., REA, B., RIO, D., SAKAMOTO, T., SMITH, D. C., STEIN, R., ST JOHN, K., SUTO, I., SUZUKI, N., TAKAHASHI, K., WATANABE, M., YAMAMOTO, M., FARRELL, J., FRANK, M., KUBIK, P., JOKAT, W. & KRISTOFFERSEN, Y. 2006. The Cenozoic palaeoenvironment of the Arctic Ocean. *Nature* **441**, 601–5.
- MOSBRUGGER, V., UTESCHER, T. & DILCHER, D. L. 2005. Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Sciences USA* **102**, 14964–9.
- PARRIS, D. C., GRANDSTAFF, B. S., DENTON, R. K. & DOBIE, J. L. 1997. *Diplocynodon* (Alligatorinae) in the Cretaceous of eastern North America. *Journal of Vertebrate Paleontology* **17**, 69A.
- PIRAS, P. & BUSCALIONI, A. D. 2006. *Diplocynodon muelleri* comb. nov., an Oligocene diplocynodontine alligatoroid from Catalonia (Ebro Basin, Lleida province, Spain). *Journal of Vertebrate Paleontology* **26**, 608–20.
- POMEL, A. 1847. Note sur les animaux fossiles de'couverts dans le département de l'Allier. *Bulletin de la Société Géologique de France* **4**, 378–85.
- RAGE, J.-C. 2006. The lower vertebrates from the Eocene and Oligocene of the Phosphorites du Quercy (France): an overview. *Strata série 1* **13**, 161–73.
- SALISBURY, S. W., MOLNAR, R. E., FREY, E. & WILLIS, P. M. A. 2006. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. *Proceedings of the Royal Society of London, Series B* **273**, 2439–48.
- SCHOUTEN, S., ELDTRETT, J., GREENWOOD, D. R., HARDING, I. & SINNINGHE DAMSTÉ, M. B. J. S. 2008. Onset of long-term cooling of Greenland near the Eocene–Oligocene boundary as revealed by branched tetraether lipids. *Geology* **36**, 147–50.
- SEYMOUR, R. S., BENNET-STAMPER, C. L., JOHNSTON, S. D., CARRIER, D. R. & GORDON, G. C. 2004. Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. *Physiological and Biochemical Zoology* **77**, 1051–67.
- STEHLIN, H. G. 1910. Remarques sur les faunules de Mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bulletin de la Société Géologique de France* **4**, 488–520.
- SWOFFORD, D. L. 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods)* (Ver 4.0b10) (Sinauer Associates, Sunderland, MA).
- THIRY, M., SCHMITT, J. M., TRAUTH, N., COJEAN, R. & TURLAND, M. 1983. Formations rouges 'sidérolithiques' et silicifications sur la bordure Nord du Massif Central. *Revue Géologique de Dynamique Géographique et Physique* **24**, 381–95.
- TRIPATTI, A. K., EAGLE, R. A., MORTON, A., DOWDESWELL, J. A., ATKINSON, K. L., BAHÉ, Y., DAWBER, C. F., KHADUN, E., SHAW, R. M. H., SHORTTLE, O. & THANABALASUNDARAM, L. 2008. Evidence for glaciation in the Northern Hemisphere back to 44 Ma from ice-rafted debris in the Greenland Sea. *Earth and Planetary Science Letters* **265**, 112–22.
- VAILLANT, L. 1872. Étude zoologique sur les crocodyliens fossiles de Saint-Gérard Le Puy. *Annales de la Société Géologique de France* **3**, 1–58.
- VASSE, D. 1992. Un crâne d'*Asiatosuchus germanicus* du Lutétien d'Issel (Aude). Bilan sur le genre *Asiatosuchus* en Europe. *Geobios* **25**, 293–304.
- VIGNAUD, P., BRUNET, M., GUEVEL, B. & JEHENNE, Y. 1996. Un crâne de *Diplocynodon* (Crocodylomorpha, Alligatoridae) de l'Oligocène inférieur de Dordogne (France). *Comptes rendus de l'académie des sciences, Paris, série II* **322**, 595–601.
- ZACHOS, J. C., SHACKLETON, N. J., REVENAUGH, J. S., PALIKE, H. & FLOWER, B. P. 2001. Climate response to orbital forcing across the Oligocene–Miocene boundary. *Science* **292**, 274–8.