New dyrosaurid crocodylomorph and evidences for faunal turnover at the K–P transition in Brazil

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The discovery of a new dyrosaurid crocodylomorph from the well-dated Palaeocene deposits of northeastern Brazil sheds new light on the evolutionary history of this extinct group of marine crocodylomorphs that have survived the Cretaceous–Palaeogene (K–P) extinction crisis. *Guarinisuchus munizi*, the most complete member of this group collected in South America so far, is closely related to the African forms, and this fact suggests that dyrosaurids had crossed the Atlantic Ocean before the K–P boundary and dispersed from there to North America and other parts of South America. This discovery also suggests that on the coast of northeastern Brazil, dyrosaurids replaced the pre-existing Late Cretaceous fauna of diversified mosasaurs, a group of marine lizards, after the K–P extinction event, becoming the main predators, together with sharks, in shallow marine Palaeocene environments. More detailed stratigraphic records and detailed dating of the deposits with dyrosaurids are necessary to correlate this particular pattern found in the ancient northeastern Brazilian coast within the evolution of the group, especially in Africa.

Keywords: crocodylomorph; Dyrosauridae; Palaeocene; K–P boundary; extinction

1. INTRODUCTION

Among the few vertebrates that survived the mass extinction event documented at the Cretaceous–Palaeogene boundary are dyrosaurids (Buffetaut 1990). These long-snouted extinct marine crocodylomorphs are known mainly from the Maastrichtian deposits of New Jersey (Owen 1849; Denton *et al.* 1997) and the Late Cretaceous to Early Palaeogene units formed by the Tethys Sea in northern and western Africa (Swinton 1950; Halstead 1975; Buffetaut 1978*a*, 1981; Brochu *et al.* 2002; Jouve 2005; Jouve *et al.* 2005*a*). Incomplete material is also known from the Palaeocene and Eocene strata of Pakistan (Buffetaut 1978*b*; Storrs 1986). In South America, dyrosaurids were previously known only by fragmentary material (Cope 1886; Argollo *et al.* 1987; Buffetaut 1991; Gayet *et al.* 1991) and some cranial material briefly mentioned in the literature (Hastings & Bloch 2007). Despite being of great interest, in part due to their survivorship across the Cretaceous–Palaeogene boundary (Buffetaut 1990), the fragmentary nature of most specimens hampers a better knowledge of the diversity and evolutionary history of the group. Furthermore, the majority of the occurrences have no detailed stratigraphic record or accurate information regarding their age (Argollo *et al.* 1987; Buffetaut 1991; Jouve *et al.* 2005*a*; Jouve 2007), a common feature particularly for the African deposits (e.g. Kellner & Mader 1997).

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Fieldwork carried out in the Poty Quarry, a limestone quarry located close to Recife in northeastern Brazil, has revealed the remains of a dyrosaurid crocodylomorph. This is the only Brazilian locality from where the remains of these marine reptiles were obtained (Kellner 1998; Kellner & Campos 1999). One possible aquatic crocodylomorph was previously found in Brazil, but is not a dyrosaurid and comes from much older deposits (Kellner 1987).

The new specimen was collected from the deposits of the Maria Farinha Formation, Danian, Paraíba Basin (figure 1*a*). The Poty Quarry is of particular interest, since it shows the most complete exposed marine section of the Cretaceous–Palaeogene transition in South America, and the associated faunal turnover across the K–P section has been well studied (Albertão *et al.* 1994; Stinnesbeck & Keller 1995; Keller 2001; Fauth *et al.* 2005; figure 1*b*).

2. SYSTEMATIC PALAEONTOLOGY

Crocodylomorpha Walker, 1970.
    Neosuchia Benton & Clark, 1988.
    Dyrosauridae de Stefano, 1903.
    Guarinisuchus munizi gen. et sp. nov.
    Etymology. Guarini from the Tupi language meaning warrior + *suchus* from the Greek language meaning crocodile; *munizi*, in honour of Geraldo da Costa Barros Muniz owing to his pioneer palaeontological studies in the Paraíba Basin.
    Holotype. Skull and mandible, ulna, cervical and caudal vertebrae, ribs, dermal scutes and isolated teeth (DG-CTG-UFPE 5723). Casts at the Museu Nacional

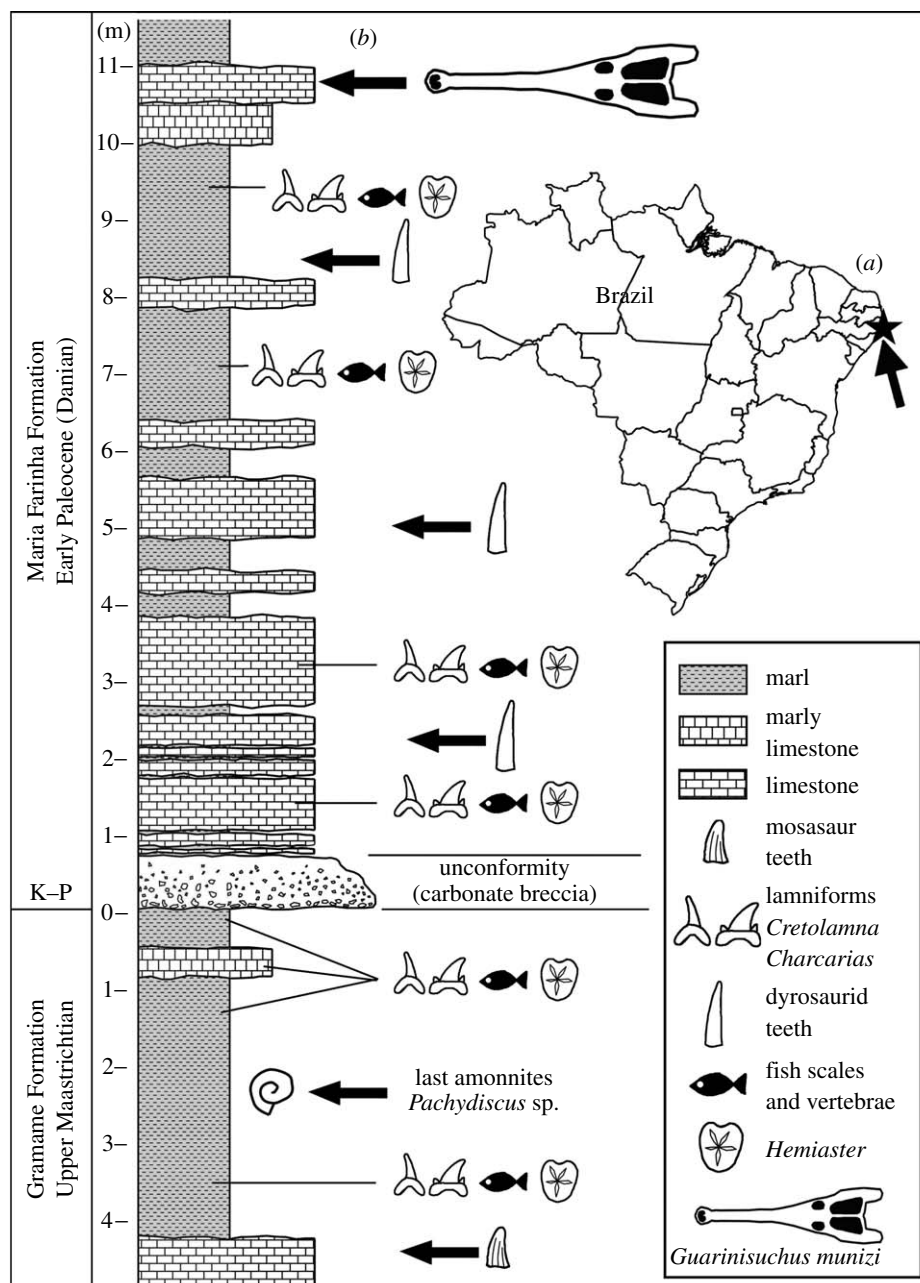This journal is © 2008 The Royal Society

Figure 1. (*a*) Location of Poty Quarry, Paraíba Basin, northeastern Brazil. (*b*) Stratigraphic section of the K–P transition at the Poty Quarry with the location where *G. munizi* was collected is indicated.

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Type locality, horizon and age. The Poty Quarry is located in the region of Paulista (7°54′47″ S,34°51′00″ W), north of Recife, Pernambuco State; Maria Farinha Formation, Paraíba Basin; Early Palaeocene (Late Danian; Albertão *et al.* 1994; Stinnesbeck & Keller 1995; Fauth *et al.* 2005).

Diagnosis. Comparatively small dyrosaurid crocodylomorph (approx. 3 m) with the postorbital region of the skull elongated; posterior margin of parietal slightly concave; elongated basioccipital with a distinct depression on the ventral surface; and a marked 'V'-shaped basioccipital in occipital view.

3. DESCRIPTION AND COMPARISON

All bones were found in one limestone block and were not articulated, suggesting that some transportation had taken place before the animal's final burial. The material is well preserved, although some signs of dorsoventral compression in the skull are evident (figure 2*a–f*).

Guarinisuchus munizi can be referred to the Dyrosauridae, which is defined as the most common ancestor of *Chenanisuchus lateroculi* and *Rhabdognathus keiniensis* and all their descendants (see the electronic supplementary material), based on the presence of exoccipital processes and the elongated upper temporal fenestra, which in this clade is always larger than the orbit (Brochu *et al.* 2002; Jouve *et al.* 2005*a*). The skull is almost complete and lacks part of the right quadrate and quadratojugal (figure 2*a–g*). The bone surface of almost all elements is ornamented with pits, shallow grooves and ridges, but not as strongly as in most dyrosaurid taxa (e.g. *Chenanisuchus*, *Sokotosuchus ianwilsoni* and *Hyposaurus rogersii*). The dorsal surface near the contact area between the premaxilla and the maxilla is partially broken. The skull is approximately
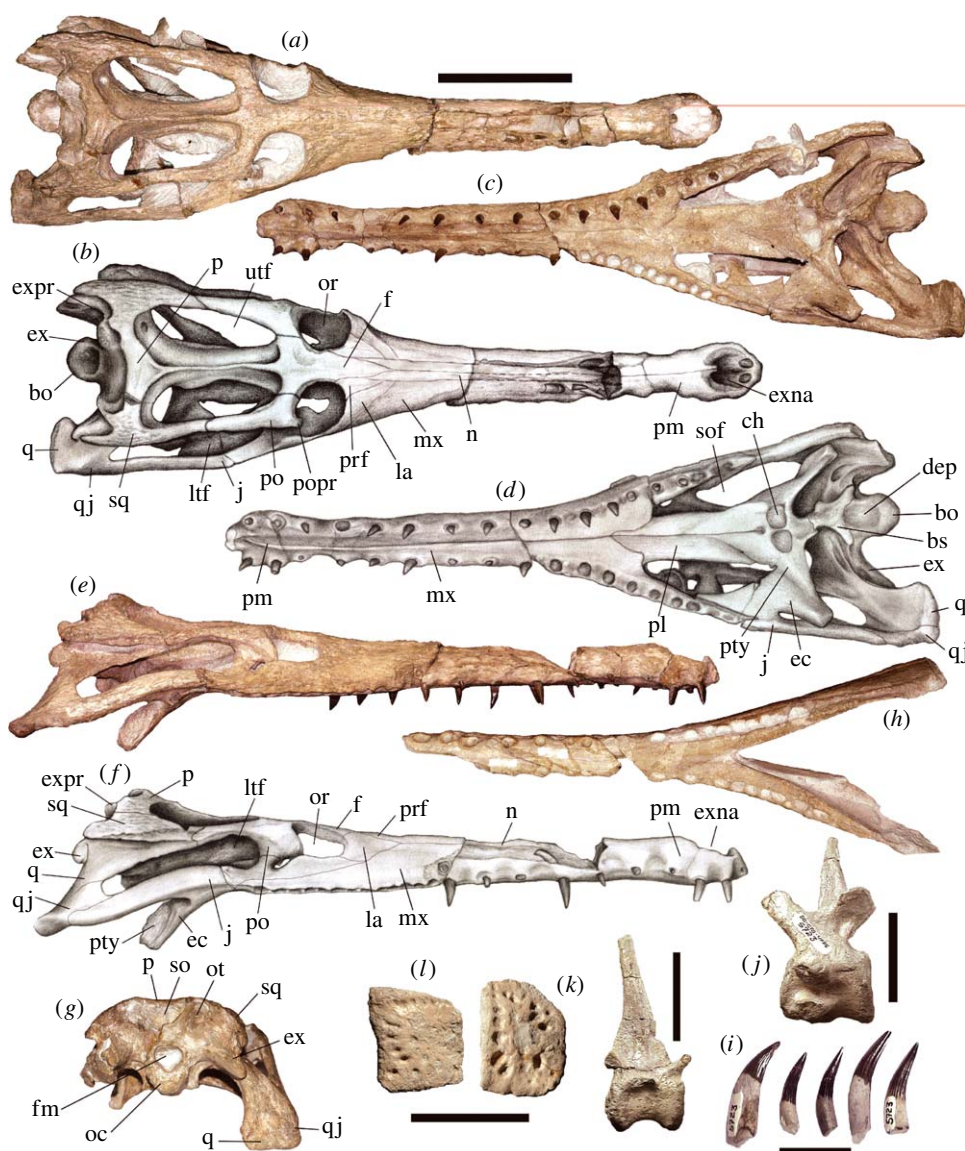
Figure 2. Material of *G. munizi* (DG-CTG-UFPE 5723). Skull in (*a,b*) dorsal, (*c,d*) ventral, (*e,f*) right lateral and (*g*) occipital views; (*h*) lower jaw in dorsal view; (*i*) isolated teeth in labial view; (*j*) cervical vertebra in right lateral view; (*k*) posterior caudal vertebra in right lateral view and (*l*) dermal scutes in dorsal view. Scale bars: (*a*)–(*h*) 10 cm, (*i*) 2 cm, (*j,k*) 5 cm, (*l*) 5 cm. bo, basioccipital; bs, basisphenoid; dep, depression; ch, choanae; ec, ectopterygoid; ex, exoccipital; exna, external narina; expr, exoccipital processes; f, frontal; fm, foramen magnum; j, jugal; la, lacrymal; ltf, lower temporal fenestra; mx, maxilla; n, nasal; oc, occipital condyle; or, orbit; ot, occipital tuberosity; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; popr, postorbital process; prf, prefrontal; pty, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sof, suborbital fenestra; sq, squamosal; utf, upper temporal fenestra.

525 mm long and its maximum width (over the quadratojugals) is 160 mm, indicating that the total length of this individual was approximately 3 m, estimated from dyrosaurid body×skull chart proportions presented by Jouve *et al.* (2005*b*). On the cervical vertebra, the suture of the centrum and the neural arch is fused while in all of the preserved caudals the sutures are open, showing that this specimen represents a sub-adult individual at the time of death. In crocodylians and relatives, the vertebrae fuse from the tail forward (Brochu 1996). Nonetheless, *G. munizi* appears to be smaller than most dyrosaurid taxa known so far except for *H. rogersii* from the Maastrichtian of the USA (Denton *et al.* 1997).

The skull has an elongated tubular rostrum, which is a typical dyrosaurid feature. The preorbital region is narrow, differing from more primitive members of this group (e.g. *Chenanisuchus*, *Sokotosuchus*) and is shorter than in

R. keiniensis, *Arambourgisuchus khouribgaensis* and *Dyrosaurus phosphaticus* (Buffetaut 1979; Jouve 2005; Jouve *et al.* 2005*a,b*). Unlike other dyrosaurids, the postorbital portion of the skull in *G. munizi* is proportionally more elongated (figure 2*a,c*).

The orbit is placed dorsolaterally and has a rather circular outline. Its posterolateral corner is cut by a well-developed anterolateral preorbital process (figure 2*a,c*). The upper temporal fenestra is elongated anteroposteriorly, which is a typical feature of dyrosaurids. Nonetheless, there is some variation in the elongation of this opening as indicated by the width–length ratio: *Guarinisuchus* and *Rhabdognathus* have the longest upper temporal fenestrae of all dyrosaurids (ratio lower than 0.4; see the electronic supplementary material). The bony bar that separates the upper temporal fenestrae is formed by the parietal and frontal. This element is not broad as in *Chenanisuchus* or

'T' shaped as in *Dyrosaurus* (Jouve *et al.* 2005*b*; figure 2*a,c*), but is very thin, unsculpted and forms a sagittal crest, similar to the condition observed in *Arambourgisuchus* and *Rhabdognathus* and differs from other dyrosaurids, including those with a thin interfenestral bony bar (e.g. *Hyposaurus*). The lower temporal fenestra is very elongated anteroposteriorly, with a concave ventral margin, less pronounced than in *Rhabdognathus aslerensis* (Brochu *et al.* 2002). Even taking into account the dorsoventral compression to which the skull was subjected to, this cranial opening appears to be more elongated than in most other dyrosaurids.

The premaxilla is slightly expanded at the distal end laterally, with the tip that bears the first premaxillary teeth slightly projected, similar to *A. khouribgaensis* and *Congosaurus bequaerti* (Jouve & Schwarz 2004), but differs from the rounded and triangular termination of *R. keiniensis* and *C. lateroculi*, respectively (figure 2*a–f*). The maxilla is long (approx. two and a half times the length of jugal) and forms most of the lateral margin of the skull. There are 12–13 rounded alveoli in each maxilla, some with the teeth *in situ*, particularly on the left side (figure 2*c–f*). One of the more striking features are the deep occlusal pits, present particularly in the posterior region of the maxillae that get less pronounced anteriorly. These pits indicate that the teeth from the upper and lower jaws alternate, forming a strong interlocking system when the jaws were closed (figure 2*c–f*). Similar deep occlusal pits were reported in *R. aslerensis* (Brochu *et al.* 2002), but in *G. munizi* they are better developed, being almost the same size as the adjacent alveoli. The preorbital bears a well-developed anterolateral process, preserved only on the right side in the present material, which is also regarded as a dyrosaurid feature (Buffetaut 1979). This process is less developed than in *D. phosphaticus* and *R. keiniensis*, and less broad than in *D. phosphaticus* (figure 2*a,b,e,f*).

In dorsal view, the posterior margin of the parietal is slightly concave, differing from all other dyrosaurids (figure 2*a,b*), although within this clade of marine crocodylomorphs this feature is variable. The primitive condition is a straight posterior parietal margin present in *C. lateroculi*, *D. phosphaticus*, *Phosphatosaurus gavialoides*, *R. aslerensis* and also in *Terminonaris* (Wu *et al.* 2001) that is regarded as the sister group of Dyrosauridae (Jouve *et al.* 2005*a*; see the electronic supplementary material). *Hyposaurus rogersii* displays a distinct V-shaped condition, in *R. keiniensis* this region presents a strong concavity and in *A. khouribgaensis* the parietals taper posteriorly showing a pointed end (Jouve *et al.* 2005*a*), all features that are regarded here as autapomorphies of the respective species. The squamosal forms the ventroposterior dorsal corner of the skull (figure 2*a,b,e,f*). The posterior margin of this bone lateral to the occipital processes is concave, a feature shared with *Rhabdognathus* (*R. keiniensis* and *R. aslerensis*) and *A. khouribgaensis*. The exoccipital processes (or tuberosities) are well developed, being larger than in *Chenanisuchus* and *S. ianwilsoni*, but smaller than in *Rhabdognathus* (Jouve *et al.* 2005*b*; figure 2*a–g*). These tuberosities are rounded and not flattened as reported in *H. rogersii* and *A. khouribgaensis* (Jouve *et al.* 2005*a*). The occipital region between the exoccipital processes is concave. The basioccipital is elongated posteriorly and shows a distinct depression on the ventral surface; in occipital view it is V shaped, features that are unique to this new taxon. The quadratojugal is laterally expanded, as in most dyrosaurids, differing from the anteroposteriorly expanded condition observed in *R. aslerensis* (Brochu *et al.* 2002; figure 2*a–g*).

The lower jaw is incomplete, lacking the distal end and the retroarticular process. As in the upper jaw, alveoli are rounded and deep occlusal pits are present on the posterior region. The mandibular symphysis is more wide than deep, differing from *C. bequaerti*, *D. phosphaticus* and *R. keiniensis* (figure 2*h*). Although not complete, we estimate the total number of the teeth present in the lower jaw similar to the upper jaw (see below), with the symphysis starting at around the 14th alveolus.

The total number of alveoli on each side of the upper jaw is 17–18, 14 out of which are confined to the preorbital region (figure 2*h*). This is less than the number of teeth reported in *R. keiniensis* (27–28, 25 preorbital), *D. phosphaticus* (25, 21 preorbital), and *C. bequaerti* (minimum 20, with 17 preorbital; Jouve & Schwarz 2004) and slightly less than *A. khouribgaensis* (21, with 16 preorbital) but more than *Hyposaurus* that has only 15 teeth (Jouve & Schwarz 2004). The teeth are long, show strong striations and unserrated anterior and posterior carinae (figure 2*i*). They lack the particular medially 'twisted' anterior carina reported in *Hyposaurus* (Denton *et al.* 1997). The anterior-most teeth are arched, curving posteriorly. They show a rounded cross-section and the posterior ones are not labiolingually compressed as are the ones reported in *C. bequaerti* (Jouve & Schwarz 2004).

The postcranial elements recovered so far agree with the general description of dyrosaurid postcranials (Schwarz *et al.* 2006), with the caudal vertebrae displaying a comparatively high neural spine (figure 2*j,k*). The dermal scutes recovered are flat, with the dorsal (external) surface ornamented by pits of different depth and the ventral surface smooth (figure 2*l*).

Until recently, only fragmentary dyrosaurid remains were reported from Brazil and Bolivia in South America. The specimens from Bolivia consist of one isolated vertebra from the El Molino Formation (Gayet *et al.* 1991), two isolated teeth, one dorsal vertebra and dermal scutes from the region of Lake Titicaca, placed in the Palaeocene (Argollo *et al.* 1987), and fragmentary material first regarded as closely related to *Sokotosuchus* aff. *ianwilsoni* from the Santa Lucía Formation, Palaeocene (Buffetaut 1991), which is presently regarded as an indeterminate dyrosaurid (Jouve 2007).

From Brazil, isolated vertebrae and teeth referred to Dyrosauridae have been reported from the Maria Farinha Formation, which is the same unit where *G. munizi* came from (Carvalho & Azevedo 1997; Gallo *et al.* 2001). Cope (1886) previously described fragmentary elements, including a lower jaw, as '*Hyposaurus derbianus*' which he regarded as coming from the Cretaceous strata of Pernambuco. However, he did not figure this specimen and no precise location was provided; so it is possible that this material might be from the Maria Farinha Formation. Furthermore, the type material of *H. derbianus* is scattered in different collections (Longbottom 1988), some of which could not be located during the preparation of this paper. In any case, the comparisons presented above shows that *G. munizi* is quite distinct from *Hyposaurus* (see the electronic supplementary material).
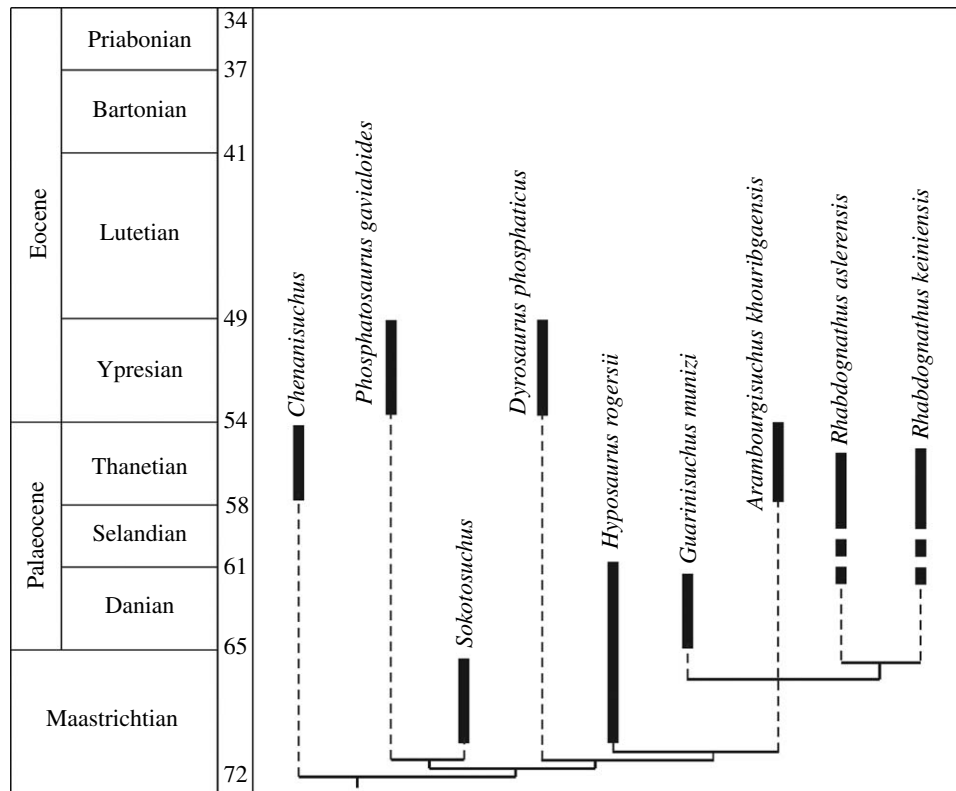
Figure 3. Temporally calibrated phylogeny of dyrosaurid crocodylomorphs based on the strict consensus tree resulting from the phylogenetic analysis (see the electronic supplementary material). Solid bars indicate known temporal ranges and dashed lines missing ranges. *Guarinisuchus munizi* from the Early Palaeocene fills the gap between the Late Cretaceous and the Late Palaeocene dyrosaurids.

4. DISCUSSION AND CONCLUSIONS

In order to access the phylogenetic position of *G. munizi*, we performed a phylogenetic analysis using a modified version of the dataset published by Jouve *et al.* (2005*a*; see the electronic supplementary material). The results indicate that the Brazilian taxon is closely related to the African forms *A. khouribgaensis* from the Palaeocene deposits of Morocco (Jouve *et al.* 2005*a*) and *Rhabdognathus* from the Palaeocene strata of Mali (Jouve 2007), although we could not precisely estimate to which of the two it is more closely related (figure 3).

The phylogenetic analysis and the precise stratigraphical position of *G. munizi* within the Maastrichtian–Palaeocene transition zone gives relevant information regarding the group's evolutionary history, and raises some possibilities regarding dyrosaurid dispersal routes. Based on the known record of dyrosaurids and their phylogenetic relationships presented here, there are two general possibilities that can account for their distribution; both take into account the origin of this group in northern Africa (Jouve *et al.* 2005*a*; figure 4). The first hypothesis advocates a dispersal route going eastwards. From there they could have reached Asia and the Benue Trough, an inland sea that stretched across the present Sahara. Before the end of the Cretaceous, dyrosaurids could have crossed the Atlantic Ocean from the western coast of Africa to the area presently corresponding to Pernambuco in northeastern Brazil, where the distance between Africa and South America was (and still is) shorter. From there they could have dispersed northwards along the coast reaching North America and other areas of the South American continent using epicontinental seas that existed at that time, including the regions of Colombia and

Bolivia. The alternative hypothesis differs by taking into account the possibility that dyrosaurids could also have dispersed westwards and then south along the marginal basins of the African coast, crossing the Atlantic Ocean from there. Those two hypotheses do not necessarily exclude each other, but more information on the dyrosaurids from the western coast of Africa is needed in order to test the second one. Theoretically, one could also argue for a northern dispersal route through which, after their origin, dyrosaurids reached Europe and then crossed the North Atlantic Ocean to North America, reaching South America from there. The present study, however, did not find any evidence for this alternative scenario, particularly since *Guarinisuchus* is more closely related to the African forms than the North American dyrosaurids. Based on the phylogenetic analysis presented here, this dispersal event must have occurred before the Maastrichtian–Palaeogene boundary.

A detailed stratigraphic work shows the presence of the K–P boundary in the Poty Quarry (Albertão *et al.* 1994; Stinnesbeck & Keller 1995; Fauth *et al.* 2005). The lower portion of the sedimentary sequence is formed by the Maastrichtian Gramame Formation that is overlain by the Early Palaeocene Maria Farinha Formation. *Guarinisuchus munizi* was found 11 m above the K–P boundary in layers whose age, established based on microfossils, is regarded as the P2 biozone of the Late Danian (Fauth *et al.* 2005), and indicates an age of 62–61 Myr ago (figure 1). Mosasaurs remains have been collected in the uppermost layers of the Gramame Formation in the Poty Quarry and four distinct clades were recognized (Mosasaurini, Globodensini, Plioplatecarpini and Prognathodontini; Price 1957; Carvalho & Azevedo 1998).
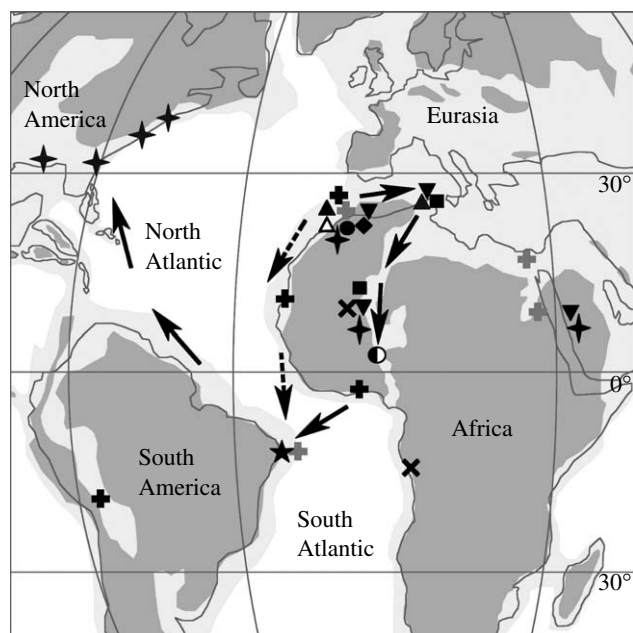
Figure 4. Palaeogeography of North America, South America, Europe and Africa during the Upper Maastrichtian–Palaeocene, with the indication of two possible dispersal routes for the Dyrosauridae. In both hypotheses, dyrosaurids have originated in northern Africa, with the first dispersal route (solid arrow) going eastwards, reaching Asia, and crossing the inland sea that stretched across the present Sahara. The second hypothesis (broken arrow) suggests that dyrosaurids could also have moved westwards and then south along marginal basins of the African coast. Before the end of the Cretaceous, they had crossed the Atlantic Ocean reaching South America in the present area of Pernambuco, dispersing from there northwards along the coast reaching North America and other areas of the South American continent. Occurrences of taxa are indicated as follows: four-point stars, *Hyposaurus*; left-filled circle, *Sokotosuchus*; star, *Guarinisuchus*; diamond, *Chenanisuchus*; circle, *Arambourgisuchus*; open triangle, *Atlantosuchus*; filled down triangles, *Rhabdognathus*; crosses, *Congosaurus*; squares, *Phosphatosaurus*; filled upright triangles, *Dyrosaurus*; light grey pluses, Dyrosauridae indet from the Cretaceous deposits; black pluses, Dyrosauridae indet from the Palaeocene deposits.

Despite intensive collection, they have not been found in the Maria Farinha Formation, corroborating the general notion that those large marine reptiles did not survive the mass extinction event of the K–P boundary.

Based on the studies of the Poty Quarry, and the collected material described here, we can suggest that at least in this region of the northeastern Brazilian margin, dyrosaurids occupied the niche of major predators left by mosasaurs after the K–P transition, becoming the major predator in shallow marine and near-shore habitats (figure 1). In the coastal deposits of New Jersey, which present an important K–P record, although dyrosaurids coexisted with mosasaurs during the Late Maastrichtian, their remains are rare, but after the K–P boundary they become more numerous, and marine crocodyliforms such as the dyrosaurids *Hyposaurus* and *Thoracosaurus*, together with lamnid sharks, became the major predators (Gallagher 2005). Also, some large sharks that are present in the Maastrichtian of the Paraíba Basin disappeared during the K–P event, but two smaller genera of lamnid sharks crossed the K–P boundary (Gallo *et al.* 2001) and coexisted with

G. munizi. It is also interesting to note that dyrosaurids diversified considerably during the Palaeocene, in contrast to the rarity of their remains in the Maastrichtian (Buffetaut 1990; Bardet 1994; Bardet *et al.* 2005). More studies, including detailed stratigraphic work in other basins, particularly in Africa where the Cretaceous–Palaeogene boundary is present as well, might shed more light on the question if the replacement of mosasaurs by dyrosaurids after the K–P transition was a local event or a global trend.

REFERENCES

Albertão, G. A., Koutsoukos, E. A. M., Regali, M. P. S., Attrep Jr, M. & Martins Jr, P. P. 1994 The Cretaceous–Tertiary boundary in southern low-latitude regions: preliminary study in Pernambuco, north-eastern Brazil. *Terra Nova* **6**, 366–375. (doi:10.1111/j.1365-3121.1994.tb00509.x)

Argollo, J., Buffetaut, E., Cappetta, H., Fornari, M., Herail, G., Laubacher, G., Sigé, B. & Vizcarra, G. 1987 Découverte de Vertébrés aquatiques présumés Paléocènes dans les Andes septentrionales des Bolivie (Rio Suches, synclinorium de Puntina). *Geobios* **20**, 123–127. (doi:10.1016/S0016-6995(87)80061-X)

Bardet, N. 1994 Extinction events among Mesozoic marine reptiles. *Hist. Biol.* **7**, 313–324.

Bardet, N., Superbiola, X. P., Iarochene, M., Bouya, B. & Amaghzaz, M. 2005 A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). *Zool. J. Linn. Soc.* **143**, 447–472. (doi:10.1111/j.1096-3642.2005.00152.x)

Brochu, C. A. 1996 Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *J. Vert. Paleontol.* **16**, 49–62.

Brochu, C. A., Bouaré, M. L., Sissoko, F., Roberts, E. M. & O'Leary, M. A. 2002 A dyrosaurid crocodyliform braincase from Mali. *J. Paleontol.* **76**, 1060–1071. (doi:10.1666/0022-3360(2002)076<1060:ADCBFM>2.0.CO;2)

Buffetaut, E. 1978a Les Dyrosauridae (Crocodylia, Mesosuchia) des phosphates de l'Eocéne inférieur de Tunisie: Dyrosaurus, Rhabdognathus, Phosphatosaurus. *Géologie Méditerranéenne* **5**, 237–256.

Buffetaut, E. 1978b Crocodilian remains from the Eocene of Pakistan. *Neues Jahrb. Geol. Paläontol. Abh.* **156**, 262–283.

Buffetaut, E. 1979 Sokotosuchus ianwilsoni and the evolution of the dyrosaurid crocodilians. The Nigerian Field Monograph, no. 1, pp. 31–41.

Buffetaut, E. 1981 Radiation évolutive, paléoécologie et biogéographie des crocodiliens Mésosuchiens. *Mém. Soc. Géol. France* **60**, 1–88.

Buffetaut, E. 1990 Vertebrate extinction and survival across the Cretaceous–Tertiary boundary. *Tectonophysics* **171**, 337–345. (doi:10.1016/0040-1951(90)90108-K)

Buffetaut, E. 1991 Fossil crocodilians from Tiupampa, (Santa Lucia Formation, Early Paleocene) Bolivia: a preliminary report. *Revista Técnica de YPFB* **12**, 541–544.

Carvalho, L. B. & Azevedo, S. A. K. 1997 Um crocodilo marinho (Mesosuchia: Dyrosauridae) no Paleoceno da Bacia Pernambuco-Paraíba, Brasil. *Ameghiniana* **34**, 532.

Carvalho, L. B. & Azevedo, S. A. K. 1998 Proposta taxônomica para os répteis marinhos (Lepidosauria, Mosasauridae) do Neocretáceo da Bacia Pernambuco-Paraíba. *Boletins do Museu Nacional* **43**, 1–9.

Cope, E. D. 1886 A contribution to the vertebrate paleontology of Brazil. *Proc. Am. Philos. Soc.* **23**, 1–20.

Denton, R. K. J., Bobie, J. L. & Parris, D. C. 1997 The marine crocodilian *Hyposaurus* in North America. In *Ancient marine reptiles* (eds J. M. Callaway & E. L. Nicholls), pp. 375–397. London, UK: Academic Press.

Fauth, G., Colin, J., Koutsoukos, E. A. M. & Bengtson, P. 2005 Cretaceous–Tertiary boundary ostracodes from the Poty quarry, Pernambuco, Northeastern Brazil. *J. South Am. Earth Sci.* **19**, 285–305. (doi:10.1016/j.jsames.2005.01.007)

Gallagher, W. B. 2005 Recent mosasaur discoveries from New Jersey and Delaware, USA: stratigraphy, taphonomy and implications for mosasaur extinction. *Geologie en Mijnbouw* **84**, 241–245.

Gallo, V., Figueiredo, F. J., Carvalho, L. B. & Azevedo, S. A. K. 2001 Vertebrate assemblage from the Maria Farinha formation after the K–T boundary. *Neues Jahrb. Geol. Paläontol. Abh.* **219**, 261–284.

Gayet, M., Marshall, L. G. & Sempere, T. 1991 The Mesozoic and Paleocene vertebrates of Bolivia and their stratigraphic context: a review. *Revista Técnica de YPBF* **12**, 393–433.

Halstead, L. B. 1975 *Sokotosuchus ianwilsoni* n.g., n. sp., a new teleosaur crocodile from the Upper Cretaceous of Nigeria. *J. Mining Geol.* **11**, 101–103.

Hastings, A. & Bloch, J. 2007 New short-snouted Dyrosaurid (Crocodylomorpha) from the Paleocene of Northern Colombia. *J. Vert. Paleontol.* **27**(Suppl. 67th Ann. Meet. Abstracts), 87A.

Jouve, S. 2005 A new description of *Dyrosaurus phosphaticus* (Thomas, 1893) (Mesoeucrocodylia: Dyrosauridae) from the Lower Eocene of North Africa. *Can. J. Earth Sci.* **42**, 323–337. (doi:10.1139/E05-008)

Jouve, S. 2007 Taxonomic revision of the dyrosaurid assemblage (crocodyliformes: mesoeucrocodylia) from the Paleocene of the Iullemmeden Basin, West Africa. *J. Paleontol.* **81**, 163–175. (doi:10.1666/0022-3360(2007)81[163:TROTDA]2.0.CO;2)

Jouve, S. & Schwarz, D. 2004 *Congosaurus bequaerti*, a Paleocene dyrosaurid (Crocodyliformes; Mesoeucrocodylia) from Landana (Angola). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **74**, 129–146.

Jouve, S., Iarochène, M., Bouya, B. & Amaghzaz, M. 2005a A new crocodyliform dyrosaurid from the Palaeocene of Morocco and a phylogenetic analysis of Dyrosauridae. *Acta Palaeontol. Polonica* **50**, 581–594.

Jouve, S., Bouya, B. & Amaghzaz, M. 2005b A short-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia), from the Palaeocene of Morocco. *Palaeontology* **48**, 359–369. (doi:10.1111/j.1475-4983.2005.00442.x)

Keller, G. 2001 The end-Cretaceous mass extinction in the marine realm: year 2000 assessment. *Planet. Space Sci.* **49**, 817–830. (doi:10.1016/S0032-633(01)00032-0)

Kellner, A. W. A. 1987 Ocorrência de um novo crocodiliano no Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. *An. Acad. Bras. Ciênc.* **59**, 219–232.

Kellner, A. W. A. 1998 Panorama e perspectiva do estudo de répteis fósseis no Brasil. *An. Acad. Bras. Ciênc.* **70**, 647–676.

Kellner, A. W. A. & Campos, D. A. 1999 Vertebrate paleontology in Brazil—a review. *Episodes* **22**, 238–251.

Kellner, A. W. A. & Mader, B. J. 1997 Archosaur teeth from the Cretaceous of Morocco. *J. Paleontol.* **71**, 525–527.

Longbottom, A. E. 1988 A note on the location of the type specimens of vertebrates from Brazil described by Cope in 1886. *J. Paleontol.* **62**, 828–832.

Owen, R. D. 1849 Notes on remains of fossil reptiles discovered by Prof. Henry Rodgers of Pennsylvania, U.S., in Greensand formations of New Jersey. *Q. J. Geol. Soc. Lond.* **5**, 380–383.

Price, L. I. 1957 Restos de mosasáurios de Pernambuco e considerações sobre a presença destes répteis na Bacia Amazônica do Brasil. *Bol. Dep. Nac. Prod. Min. Brasil* **169**, 1–29.

Schwarz, D., Frey, E. & Martin, T. 2006 The postcranial skeleton of the Hyposaurinae (Dyrosauridae; Crocodyliforms). *Palaeontol.* **49**, 695–718. (doi:10.1111/j.1475-4983.2006.00563.x)

Stinnesbeck, W. & Keller, G. 1995 Environmental changes across the Cretaceous–Tertiary boundary in northeastern Brazil. In *Cretaceous–Tertiary mass extinctions: biotic and environmental changes* (eds N. MacLeod & G. Keller), pp. 451–469. New York, NY: Norton.

Storrs, G. W. 1986 A dyrosaurid crocodile (Crocodylia, Mesosuchia) from the Paleocene of Pakistan. *Postilla* **197**, 1–16.

Swinton, W. E. 1950 On *Congosaurus bequaerti* Dollo. *Annales du Musée du Congo Belge* **4**, 1–37.

Wu, X. C., Russell, A. P. & Cumbaa, S. L. 2001 *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *J. Vert. Paleontol.* **21**, 492–514. (doi:10.1671/0272-4634(2001)021[0492:TACNMF]2.0.CO;2)