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ORIGINAL PAPER

A new neosuchian with Asian affinities from the Jurassic of northeastern Brazil

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Abstract Phylogenetic relationships near the origin of extant crocodylians are weakly supported, and this lack of resolution makes for poor estimates of taxonomic and morphological diversity. Previously known taxa are found throughout the Cretaceous in Laurasia and at a few sites from Brazil, Australia, and northern Africa. Here, we report *Batrachomimus pastosbonensis* gen. et sp. nov. from the Late Jurassic of northeastern Brazil, which is deeply nested within Neosuchia and associated to the Cretaceous Asian paralligatorids. The new taxon predates all other members of Paralligatoridae and its immediate sister group (including Eusuchia) by 30 million years. A nearly complete skull, osteoderms, and limb bones were recovered, and autapomorphies of *B. pastosbonensis* include a scalloped lateral margin of the rostrum in dorsal view, unsculpted alveolar margin at the caudalmost portion of the maxilla, blunt lateral prongs on the jugal at the base of the postorbital bar, hourglass shaped choanae, and pterygoid choanal septum extended between the palatal shelves of the palatines. The crocodyloid-like skull proportions and the slender, conical teeth suggest an amphibious and piscivorous life history to this 1 m long animal.

Keywords Jurassic · Neosuchia · Crocodyliformes · Palaeobiogeography · Pastos Bons Formation · Maranhão

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Introduction

The origin of extant crocodiles lies within a set of amphibious, Cretaceous forms near the base of Eusuchia. Most are relatively small-bodied, and all have broad snouts that are either elongate or abbreviated. The extremely elongate snouted taxa, such as *Isisfordia* and *Laganosuchus*, have a piscivorous dentition, whereas the short snouted taxa range from durophagous, such as *Hylaeochampsa*, to forms with reduced slender teeth, such as *Pietraroiasuchus* and *Pachycheilosuchus*. These taxa are predominantly from Laurasian deposits, although some Gondwanan forms are found in Australia (Salisbury et al. 2006), Brazil (Salisbury et al. 2003), and North Africa (Holliday and Gardner 2012). Paralligatorids (Konzhukova 1954) form a small group of advanced neosuchians close to the origin of Eusuchia previously known only from late Early to Late Cretaceous deposits of central east Asia. This clade includes *Rugosuchus nonganensis* from northeastern China (Wu et al. 2001), as well as various species attributed to the genus *Shamosuchus* from China, Mongolia, and Uzbekistan (Storrs and Efimov 2000; Pol et al. 2009). Here, we report a new neosuchian of putative paralligatorid affinities from the Late Jurassic of northeastern Brazil (Fig. 1) that not only extends the geographical range of paralligatorids into Gondwanan landmasses but also provides the earliest record of the clade composed of Paralligatoridae and its immediate sister group (including Eusuchia).

Systematic paleontology

Crocodyliformes Hay, 1930
Neosuchia Clark, 1986
Paralligatoridae Konzhukova 1954
Batrachomimus pastosbonensis new genus and species

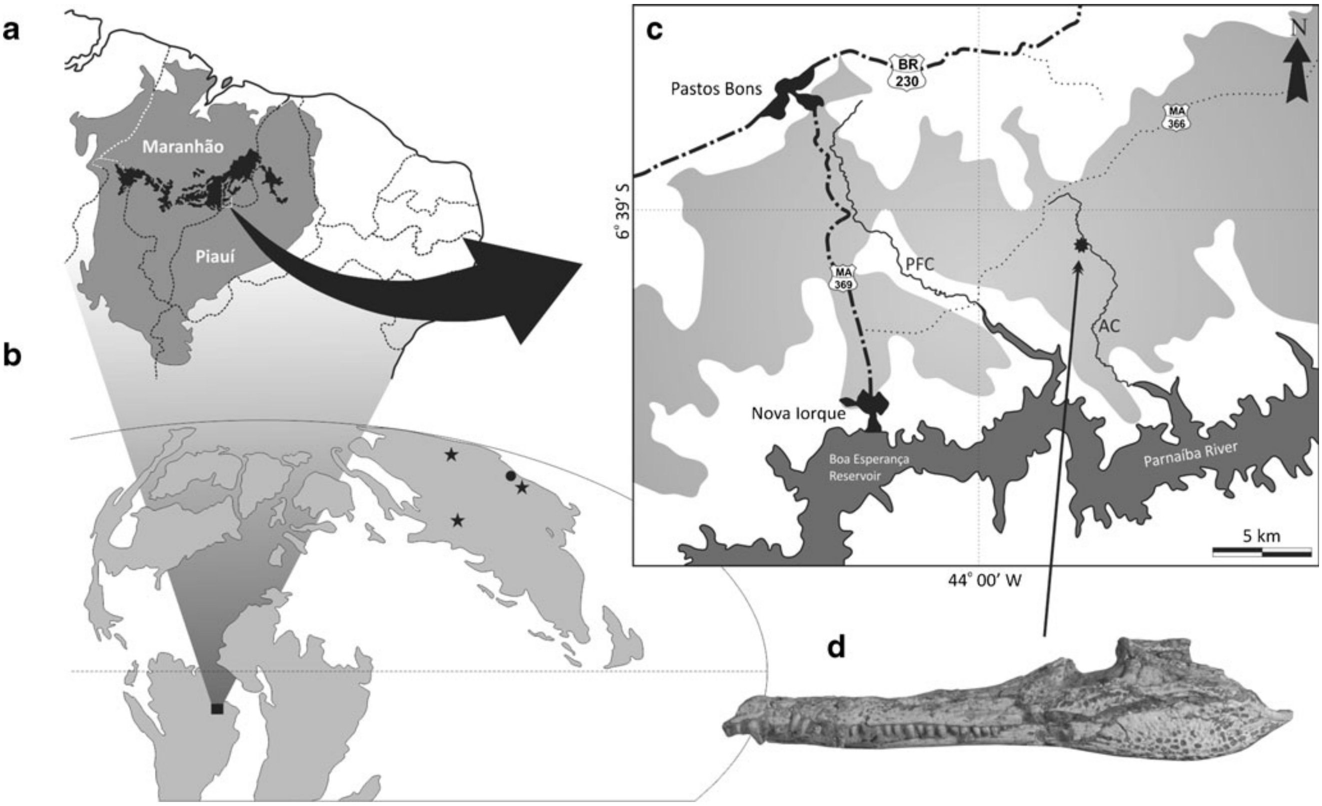

Fig. 1 **a** Map of northeastern Brazil showing the extension of the Parnaíba Province (*in gray*) and the surface distribution of the Corda and Pastos Bons Formations (*in black*). **b** Paralligatorid occurrences plotted on an early Late Cretaceous paleogeography map; *stars Shamosuchus* spp., *circle R. nonganensis*. **c** Map of the Pastos Bons area showing the type locality of *B. pastosbonensis* (*star*) and the surface distribution of the Pastos Bons Formations (*gray*). **d** Holotypic skull of *B. pastosbonensis* (LPRP/USP-0617) in lateral view. *AC* Altamira creek, *PFC* Pedra de Fogo creek

Etymology The generic epithet (batrachian mimic) alludes to the fact that the type and only known specimen was firstly believed to represent a temnospondyl "amphibian" from the Permian Pedra de Fogo Formation and also highlights the idea that from the Jurassic onwards, Crocodyliformes somewhat replaced Triassic temnospondyls in their amphibious/piscivorous habits. The specific name refers to the stratigraphic provenance (see below) of the fossil.

Holotype LPRP/USP-0617 (Laboratório de Paleontologia, FFCLRP, Universidade de São Paulo, Ribeirão Preto): partial skull, lacking most of the skull table, neurocranium and the left temporal region, nearly complete mandibles (Figs. 2 and 3), and disarticulated elements of the body armor and limbs.

Type locality and horizon Grayish sandstones of the Pastos Bons Formation, Alpercatas Basin (Góes and Feijó 1994; Santos and Carvalho 2004), exposed at a previously unexplored site in the Altamira creek area (43°57′09.08″W, 6° 39′48.24″ S) about 15 km northeast of Nova Iorque, Maranhão, Brazil (Fig. 1). Sequence stratigraphy, microfossils, and palynological data (Góes and Feijó 1994; Gallo 2005) indicate an Oxfordian-Kimmeridgian (Late Jurassic) age for the Pastos Bons Formation.

Diagnosis Distinguished from all other Crocodyliformes by the following unique set of traits (autapomorphies marked with asterisk): scalloped lateral margins of the rostrum, including premaxilla, maxilla, and jugal; premaxilla with elongated caudodorsal process reaching the level of the fifth maxillary tooth; maxilla with unsculptured lateral surface restricted to the caudalmost portion of the alveolar margin*; fully closed antorbital and mandibular fenestrae; laterally expanded caudal portions of nasal that do not form a continuous lateral curve; jugal crest extending from the caudal tip of the bone to the level of the rostral margin of the orbit; blunt lateral prongs on jugal at the base of postorbital bar; choanae constricted at midlength to form an hourglass shape*; choanal septum of pterygoid extending rostraly between the palatal shelves of the palatines to the level of the rostral edge of the suborbital fenestra*; and angular extending further rostraly (beyond the orbital margin).

Description

B. pastosbonensis is a small neosuchian with a 20-cm long skull and about 1 m of estimated body length. The premaxilla has an elongate caudodorsal process reaching the level of the fifth maxillary tooth. There are five premaxillary teeth, the

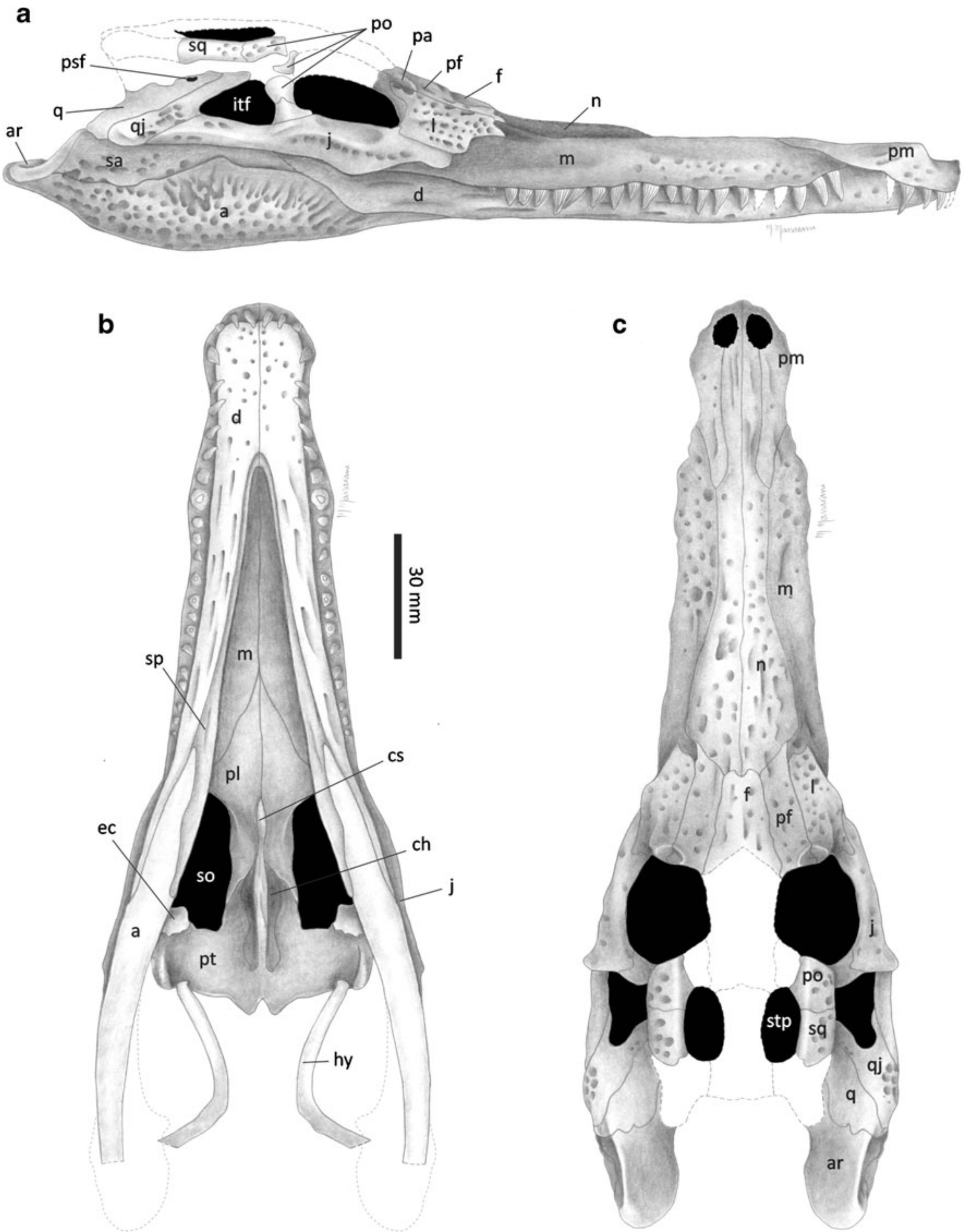

Fig. 2 *B. pastosbonensis* (LPRP/USP-0617). Reconstruction of the holotypic skull (mirrored from the preserved parts on both sides) in **a** right lateral, **b** ventral, and **c** dorsal views. *a* angular, *ar* articular, *ch* choanal aperture, *cs* choanal septum, *d* dentary, *ec* ectopterygoid, *f* frontal, *j* jugal, *hy* hyoid, *itf* infratemporal fenestra, *l* lacrimal, *m* maxilla, *n* nasal, *pa* palpebral articulation, *pf* prefrontal, *pl* palatine, *pm* premaxilla, *po* postorbital, *psf* preotic siphoneal foramen, *pt* pterygoid, *q* quadrate, *qj* quadrate-jugal, *sa* surangular, *so* suborbital fenestra, *sp* splenial, *sq* squamosal, *stf* supratemporal fenestra

fourth one being the largest. The maxilla forms most of the rostrum, which corresponds to more than 60 % of the skull length and has an extremely low profile in lateral view (Figs. 2 and 3). The antorbital fenestra is completely obliterated, as in most neosuchians and other remotely related forms (Pol et al. 2009; O'Connor et al. 2010; Montefeltro et al. 2011; Clark 2011; Pol and Powell 2011). The alveolar process of the maxilla bears over 20 conical teeth, which

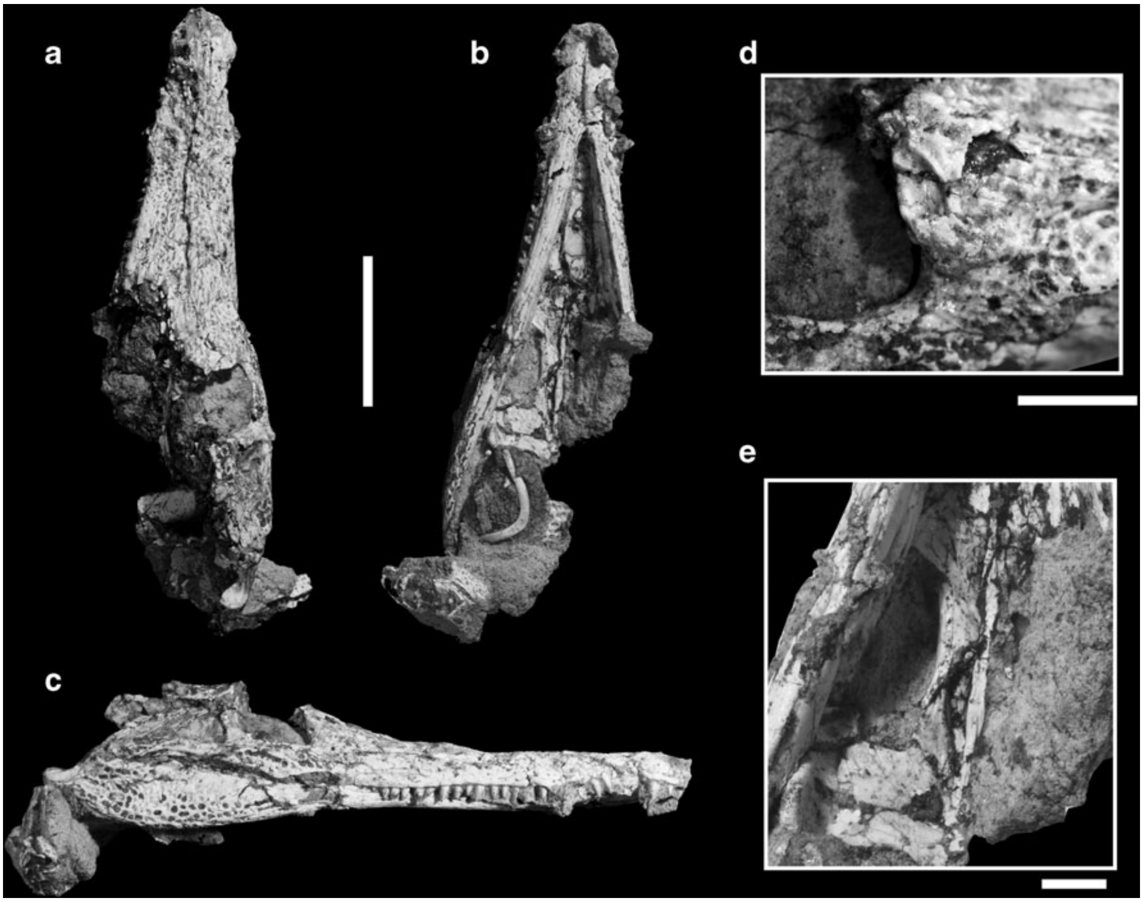

Fig. 3 *B. pastosbonensis* (LPRP/USP-0617). Skull in **a** dorsal, **b** ventral, and **c** right lateral views, structure ventrolateral to the caudal tip of the right lower jaw corresponds to sediments with preserved osteoderms. Details of Paralligatoridae skull synapomorphies: **d** articular facet for the anterior palpebral at the rostral border of the right orbit and **e** interfenestralis bar in the palate

form a gentle double wave of size variation. As in most dorsal and lateral skull elements, the maxilla is heavily sculptured with pits, except at the caudal portion of the alveolar region. This differs from protosuchids, notosuchians, and hylaeochampsids, the unsculptured region of which extends along most of alveolar margin. The palatal process of the maxilla meets its counterpart along the entire medial margin, forming the rostral portion of the secondary palate. The nasals are unfused, restricted to the top of the rostrum, and clearly expanding into the external nares. The lacrimal forms the rostroventral corner of the orbit, but does not extend rostral to the prefrontal nor contacts the nasal. The lacrimal-prefrontal suture bisects the articulation facet for the anterior palpebral, which forms a shallow hemispherical depression bordered by elevated rims, as in *Shamosuchus djadochtaensis* (Pol et al. 2009). The rostral portions of the frontals are flat with no evidence of neither transverse nor sagittal ridges.

The postorbital separates the orbit from the supratemporal fenestra, and its ventral process contacts the ascending process of the jugal, forming a cylindrical and medially inset postorbital bar. A longitudinal ridge extends along most of the dorsal edge of the rostral and caudal rami of the jugal. This is typical of derived notosuchians, but is also seen in some neosuchians, such as *Shamosuchus* and *Rugosuchus* (Storrs and Efimov 2000; Pol 2003, 2009; O'Connor et al. 2010; Montefeltro et al. 2011). The rostral ramus of the jugal is nearly twice as long and deep as the caudal ramus and has a distinct ventral expansion below the midlength of the orbit. The quadratojugal forms the entire caudal margin of the infratemporal fenestra, but does not emit a *spina quadratojugalis* within this aperture. Its ornamentation is restricted to the ventral portion where the bone is more expanded and reaches the quadrate articular region. It does not contribute to the mandibular joint (Figs. 2 and 3), which is weakly divided into a larger lateral and a smaller medial hemicondyles. The flattened rostrodorsal process of the quadrate expands into the temporal region, and it is pierced by an elliptical preotic siphoneal foramen close to the smooth quadratojugal suture.

The paired palatines bear an expanded wedge-like rostral portion, which reduces the participation of the maxillae in the rostral edge of the suborbital fenestrae. They form most of the rostral margin of the choanal aperture, which is at the level of the middle of the suborbital fenestrae. As in

Mahajangasuchids and some advanced neosuchians (Turner and Buckley 2008; Pol et al. 2009), the pterygoid forms most of the lateral portion of the choanal opening, as well as a small part of its rostral edge. The choanal septum is formed by a rostral continuous extension of the pterygoid, which extends the entire length of the choana and wedges between the palatal shelves of the palatines to the rostral margin of the suborbital fenestra. The choanal opening is hourglass shaped with a transverse constriction at its midlength. The ectopterygoid is incompletely preserved but seems to be restricted to the rostrolateral corner of the pterygoid wing. A slim and bowed *cornu brachiale* I of the right hyoid is preserved in approximate life position (Figs. 2 and 3).

The lower jaw of *B. pastosbonensis* is low at its alveolar section, but expands considerably at the level of the angular and surangular. The ventral margin of this expanded area is markedly curved and has a strongly ornamented outer surface composed by rounded and elongated pits. The mandibular symphysis is elongated, reaching the level of the fifth maxillary tooth, with little participation of the splenial (Figs. 2 and 3). There is no vestige of a mandibular fenestra, a rather uncommon trait among mesoeucrocodylians (Norell and Clark 1990; Wu et al. 2001; Company et al. 2005; Pol et al. 2009; Young et al. 2010), but present in a broad range of advanced neosuchians (Adams 2013). The splenial extends caudally as a flat vertical element medially covering most of the dentary. The angular occupies most of the caudal portion of the lower jaw, but does not reach the caudal end of the retroarticular process. Ventrally, it extends beyond the rostral margin of the orbit. The glenoid fossa corresponds in size to the quadrate condyles and is bound caudally by a buttress that limits the rostrocaudal jaw movements (Gomani 1997; Ortega et al. 2000; Ősi and Weishampel 2009). As in *S. djadochtaensis* and *Rugosuchus* (Pol et al. 2009), the broad and short retroarticular process extends from the mid-height of the caudal edge of the mandible. The dorsal armor of *B. pastosbonensis* is formed by two series of paravertebral osteoderms found semiarticulated to the skull. The elements are rectangular (less than three times broader than long) to squared-shape, have a midline keel along most of their length, and lack a rostrolateral prong.

Phylogenetic analyses and discussion

To investigate the affinities of *B. pastosbonensis*, we revised and combined a series of recent phylogenetic studies of fossil Crocodyliformes (Sereno and Larsson 2009; Turner and Sertich 2010; Andrade et al. 2011; Pol et al. 2012); see the Electronic Supplementary Material. The retrieved topology

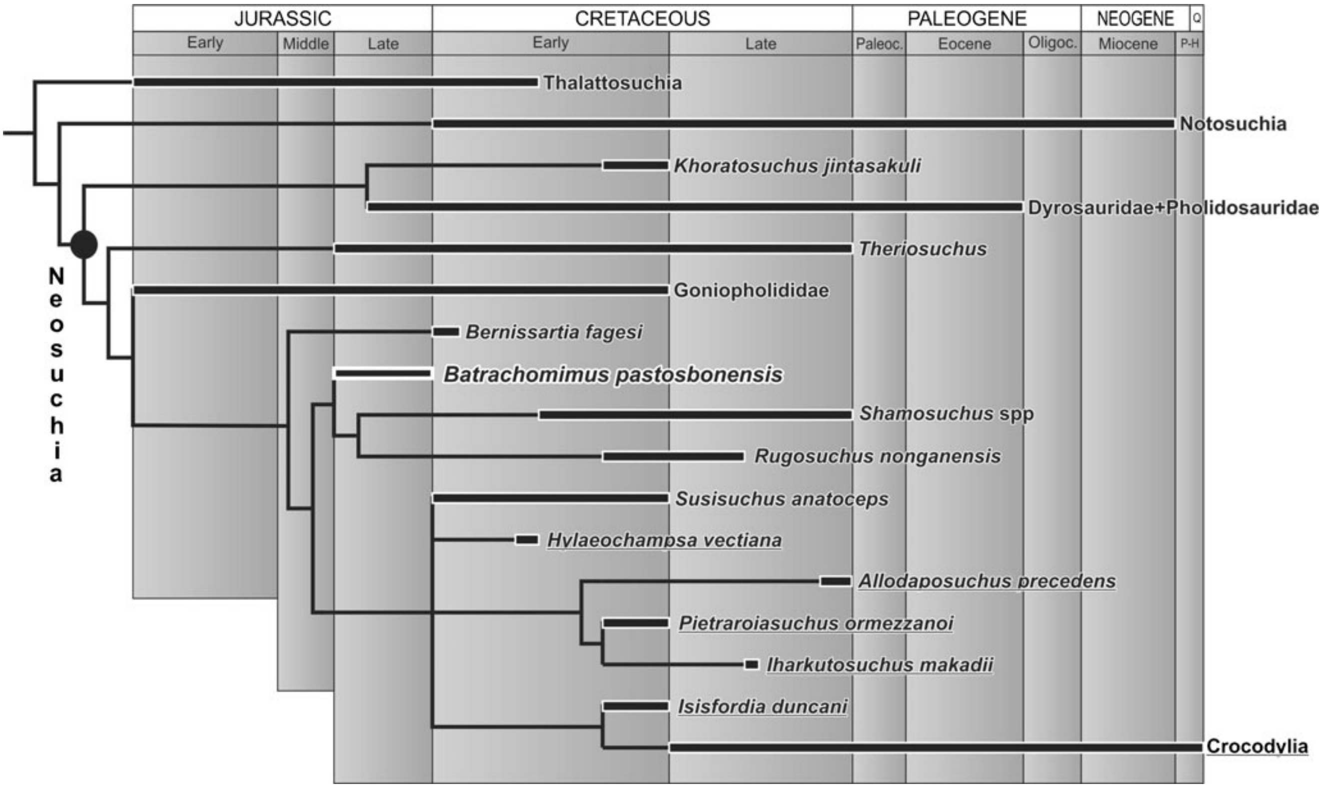

Fig. 4 Time calibrated phylogeny of near Eusuchia neosuchians derived from the strict consensus of 142 most parsimonious trees showing the relations of *B. pastosbonensis* within Crocodyliformes. Chronological distribution of major groups based on various sources and not restricted to the occurrence of taxa included in the analysis. *Q* quaternary, *P-H* pliocene-holocene

(Fig. 4) is not fully congruent with any of the previously published hypotheses, but most of the recovered clades have been formerly identified. As the sister group of the Asian Paralligatoridae, *B. pastosbonensis* is deeply nested within Neosuchia (sensu Larsson and Sues 2007). The Paralligatoridae clade is sister to a group congregating uncontroversial eusuchians (Crocodylia and hylaeochampsids), *Susisuchus anatoceps* and *Isisfordia duncani*. Given the ambiguous phylogenetic arrangement within that clade, the traditional circumscription of Eusuchia (e.g., Benton and Clark 1988; Salisbury et al. 2006; Buscalioni et al. 2011) cannot be strictly applied. In addition, *Bernissartia*, goniopholidids, and atoposaurids are successively more distant outgroups to Eusuchia plus Paralligatoridae, whereas *Khoratosuchus*, pholidosaurids, and dyrosaurids form the basal monophyletic split of Neosuchia. Thalattosuchians represent a basal radiation of mesoeucrocodylians and the sister group of the dichotomy including Notosuchia (sensu Sereno et al. 2001) and Neosuchia. Notosuchians encompass Sebecia (sensu Larsson and Sues 2007), including sebecids, peirosaurids, mahajangasuchids, and *Doratodon*, as well as a branch formed by the “traditional notosuchians” (including a monophyletic *Araripesuchus*) and baurusuchids.

Paralligatorid synapomorphies include articular facet for the anterior palpebral forming a shallow hemispherical depression bordered by elevated rims and interfenestralis bar between the suborbital fenestrae flared at both ends. Mook (1924) first described the lacrimal ridges of *S. djadochtaensis*, latter reinterpreted as a depression on the lacrimal and prefrontal (Pol et al. 2009). The homology of this unique structure to the articular facet for the anterior palpebral of most crocodyliforms is ambiguous (Pol et al. 2009; Turner and Sertich 2010), but assumed here based on topographic criteria. Ridges close to the palpebral facet are also seen in some Goniopholididae, but in a different configuration (Andrade and Hornung 2011).

The flared ends of the interfenestralis bar appeared independently several times in the evolution of Crocodyliformes, but in Paralligatoridae, the bar is flared simultaneously at both ends. In contrast to *S. djadochtaensis*, which has both ends equally flared, *B. pastosbonensis* has the rostral portion of the bar much more flared. At the caudal end, the expansion is limited to lateral bulges, as in *R. nonganensis*, and unlike the expansion formed by the interfenestralis bar in *S. djadochtaensis*. In addition, the rostral boundary of the caudal expansion is at the level of the palatine/pterygoid palatal suture in all analyzed paralligatorids.

The evolution of advanced neosuchians remains elusive in terms of geographic origins and patterns of lineage splitting (Norell and Clark 1990; Clark and Norell 1992; Salisbury et al. 2006), partly due to a scarce fossil record in the southern hemisphere. Indeed, considering its provenance and inferred phylogenetic position, *B. pastosbonensis* fulfills an important gap in the evolutionary history of Crocodyliformes. In addition, tetrapods as a whole are also not particularly well sampled in the Jurassic of Gondwana (Rauhut and Lopez-Arbarello 2008), hampering the proposal of robust palaeobiogeographic scenarios. Yet, previous to the discovery of *B. pastosbonensis*, paralligatorids were only known from the late Early–Late Cretaceous of eastern Laurasia (Pol et al. 2009). Accordingly, the new taxon indicates not only that paralligatorids are older than previously known, but also that the group either expanded its range of occurrence across the Turgai and Tethys seaways (Upchurch et al. 2002) or was present in the related landmasses prior to the formation of those barriers. The last hypothesis better fits the vicariance model proposed for Mesozoic Crocodyliformes (Turner 2004) and also follows classical works that suggest high levels of Laurasian and Gondwanan endemism among Cretaceous tetrapods (Bonaparte and Kielan-Jaworowska 1987), which implies that clades congregating Laurasian and Gondwanan taxa are more likely to have Jurassic first appearance data. On the contrary, the scenario of Early Cretaceous dispersion better fits proposed high levels of faunal cosmopolitanism at that time interval (Barrett et al. 2011; Benson et al. 2013) than the alternative restriction of Gondwanan biotic interchange with European landmasses (Ezcurra and Agnolín 2012). Indeed, an Early Cretaceous wide-reaching distribution of near Eusuchia neosuchians (Martin and Delfino 2010) represents the continuation of Jurassic biogeographic patterns (Rauhut 2010), which may also explain the broader distribution of other tetrapod clades (Choiniere et al. 2012; Benson et al. 2012).

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