A New Sebecid from the Paleogene of Brazil and the Crocodyliform Radiation after the K–Pg Boundary

Alexander W. A. Kellner1*, André E. P. Pinheiro2, Diogenes A. Campos3

1 Laboratório de Sistemática e Tafonomia de Vertebrados Fósseis - Departamento de Geologia e Paleontologia, Museu Nacional - Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, 2 Laboratório de Macrofósseis - Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, 3 Museu de Ciências da Terra, Serviço Geológico do Brasil - Companhia de Pesquisa de Recursos Minerais, Rio de Janeiro, Brazil

Abstract
A new crocodyliform, Sahitisuchus fluminensis gen. et sp. nov., is described based on a complete skull, lower jaw and anterior cervical vertebrae collected in the Sáo José de Itaboraí Basin of Rio de Janeiro, Brazil. The specimen is one of the best preserved crocodyliforms from Paleocene deposits recovered so far and represents a sebecosuchian, one of the few clades that survived the Cretaceous–Paleogene biotic crisis. The new taxon is found in the same deposit as an alligatoroid, a group that experienced large diversification in the Paleogene. The sebecosuchian record suggests that after the Cretaceous–Paleogene biotic crisis, the less specialized members of this clade characterized by a higher number of teeth compared to the baurusuchid sebecosuchians survived, some having terrestrial habits while others developed a semi-aquatic life style (e.g., Lorasuchus). Starting in the Eocene, sebecid sebecosuchians became specialized with a more accentuated oreinatrophy as observed in Sebecus and in Langstonia, but not showing the typical reduced dentition developed by the Cretaceous baurusuchid sebecosuchians. The basal position of Barinasuchus arveloi, a high-snouted Miocene sebecid, indicates the occurrence of an independent lineage sometime after the K-Pg biotic crisis that developed accentuated oreinatrophy, suggesting a more complex history of the post-K-Pg crocodyliform radiation.

Introduction
Currently crocodyliforms are worldwide distributed in tropical and subtropical regions in relative low numbers and diversity, consisting of 24 to 30 species (e.g. [1]). All are considered semiaquatic ambushers but their fossil record reveals a much richer evolutionary history in terms of anatomy and ecomorphosphates [2,3]. Particularly during the Cretaceous, the diversity of those reptiles was much higher and they occupied several distinct niches.

As a natural question, researchers tried to understand the crocodyliform decrease in diversity after the Cretaceous–Paleocene (K-Pg) extinction crisis but this discussion is hampered by the scarce nature of their remains in Paleocene deposits (e.g. [4]). Besides the marine dyrosaurids that have survived the K-Pg boundary and diversified during the Paleocene (e.g. [5,6]), there are only a limited number of Paleocene specimens described so far, most of which are fragmentary and poorly preserved (e.g. [4,7–9]). This contrasts with the high abundance of Late Cretaceous crocodyliforms, particularly in Brazil, which is even higher than in other Gondwanan areas.

During the exploration of the Sáo José de Itaboraí Basin (Rio de Janeiro State, Southeast Brazil) that lasted for about five decades and ended in 1984 [10], hundreds of fossil vertebrates were collected (Figure 1). The vast majority is housed at the Earth Science Museum (now at the Companhia de Pesquisa de Recursos Minerais – CPRM), in Rio de Janeiro, and consists of fragmentary remains representing mainly mammals (e.g. [11,12]). However, some reptiles have also been collected, including the remains of crocodyliforms [13,14], with only one species formally proposed so far [15].

Among the few well preserved and more complete crocodyliform material is an almost complete skull and lower jaw (MCT 1730-R) that was briefly mentioned (but never figured) in the literature [8,13,16] and remained undescribed until now. This specimen represents a new taxon, Sahitisuchus fluminensis gen. et sp. nov., and shows that during the Paleocene the Sáo José de Itaboraí crocodyliform fauna was composed by rather primitive (i.e., Sebecosuchia) and more derived (Alligatoridae) post-K-Pg taxa. Such a combination of sebecosuchians and eusuchians has not been previously reported in any deposit so far.

Materials and Methods
Phylogenetic Analysis
In order to access the phylogenetic position of Sahitisuchus fluminensis gen. et sp. nov., a phylogenetic analysis was performed using the data matrix published by Pol et al. (2012) [17]. Regarding Sebecus, we have followed Paullillo & Linares [9], who have restricted this genus to the type species (Sebecus icarohinus) and regarded “S”. haulemi as belonging to the genus Langstonia. A total of 89 crocodyliform taxa including the new species and 347
characters were used. Parsimony analyses using TNT [18] with heuristics search strategy (10,000 replicates of Wagner trees, 15,000 max. tree in memory) by TBR algorithm were performed. The analyses were run using unordered and ordered characters (1, 5, 6, 10, 23, 37, 43, 44, 45, 49, 63, 67, 69, 73, 77, 79, 86, 90, 91, 96, 97, 104, 105, 106, 108, 116, 126, 140, 142, 143, 149, 167, 176, 182, 197, 226, and 339). Information for *Sahiti* suchus fluminensis* gen. et sp. nov. used in the data matrix [17] is as follows: 10[0/1]?????12 ???0?-000 1101[0/1]00? 010022110 100111?11? 1101010?10 
20103[1/2]12- [2/3]10?101211 ?????0?1? 20?????1?2?[1/2]00?0?0 [0/1]10 
01?????0? ??200000 10[0/1]2212001 010[0/1]11120 
?1009110- 1701??110 
[0/1]?1000000 0101?100 0001[0/1]0001 01?1000000 
????0?000 010000?0 2090002? -1000020? -?????0010 ??????0/1]00 00010102? ????????? 
????????? ?????????? ?????????? 
For more information see Supporting Information (Data S1, Figures S1 and S2).

**Nomenclatural Acts**

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”. The LSID for this publication is: urn:lsid:zoobank.org:pub:322EE489-D9D2-4CE6-9DAF-36E30C03881D. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

No permits were required for the described study, which complied with all relevant regulations. See appropriate section of Systematic Paleontology for locality, stratigraphic, repository and specimen number.

**Results**

**Systematic Paleontology**

**Mesoeuocrocdylia** Whestone & Whybrow, 1983 [19], sensu Benton & Clark, 1988 [20]

**Sebecosuchia** Simpson, 1937 [7]

**Sebecidae** Simpson, 1937 [7]

**Sahiti* suchus fluminensis* gen. et sp. nov.** urn:lsid:zoobank.org:act:10A4487-436F-4509-BFDD-42B4DF68B177

**Derivation of name.** Generic name *Sahiti* comes from the Xavante culture (sah ti), one of the indigenous Brazilian inhabitants, meaning “to be angry” or “to be brave”, in allusion to warriors; and *suchus*, refers to the Egyptian crocodile god. Specific name *fluminensis* is a latinization of Fluminense, designation of citizens born in the Rio de Janeiro State.

**Type species.** Almost complete skull and lower jaw, protruding, intercenter, the axis and the 3rd cervical vertebra (MCT 1730-R), housed at the Museu de Ciências da Terra, Companhia de Pesquisas de Recursos Minerais (CPRM), Rio de Janeiro, Brazil (cast at the Museu Nacional/UFRJ - MN 4711-V).
Type locality, and horizon and age. São José Farm, São José de Itaboraí Municipal District, ENE in the Rio de Janeiro Metropolitan Area (SE Brazil; 22°50’50”S and 42°52’30”W). Collected in the S2 sequence [21]; Itaboraian SALMA (South American Land Mammals Age), middle Upper Paleocene, 58.2-56.5 Ma [22].

Diagnosis. Sebecid crocodyliform with the following autapomorphies: mandible lacking external mandibular fenestra; and odontoid process fused to the axis with vertical anterior surface that lacks medial processes. The new species can be further distinguished from other sebecids by the following combination of characters: infraorbital jugal region with shallow ventrolateral depression (shared with *Lorosuchus*); shallow elliptical depression on the posterior surface of the quadrate close to the craniomandibular articulation (shared with *Sebecus icaerhinus*); rough and rugose dorsal edge of supratemporal fossa (shared with *Sebecus icaerhinus*); sharp, semilunate exoccipital posterior processes, directed medially (shared with *Ayllusuchus*); jugal posterior process higher than anterior process and lateral expanded (shared with *Bretesuchus*); rough longitudinal ridge on the lateroventral edge of angular and dentary, ending close to the mandibular symphysis level (shared with *Bretesuchus*, *Sebecus*).

Description and Comparisons

Overall the material of *Sahitysuchus fluminensis* is well preserved consisting of the skull, lower jaw and cervical elements...
Although some dorsoventral crushing is observable it was not severe to affect the shape of most cranial elements, including the rostral end that kept most of original anatomy. The most affected area was the more posterior portion of the skull, with some elements, particularly the supraoccipital displaced towards the foramen magnum.

The premaxillae and the region of the external nares were broken off and the skull was slightly compressed dorsoventrally during preservation. The lower jaw is occluded with the skull and some bones lack the external bone cortex. In dorsal view, the skull of *Sahitisuchus fluminensis* is elongated, showing two slight constrictions at about the level of the 5th and 11th maxillary alveoli (Figures 2A, B). It differs from *Sebecus icacrahus* and *Stolokrosuchus* by being comparatively shorter [23,24], but not as short as *Lorosuchus* [4]. *Sahitisuchus* does not show the same oreinostral condition as *Sebecus*, *Barinasuchus*, *Bretesuchus*, *Zulmasuchus* and *Langstonia* [8,9,16,23,25].

**Cranial bones**

The skull-roof is flat and rectangular, being wider than long. The supratemporal fossa is much larger than the supratemporal fenestra (Figures 2A, B). This fossa is about three times smaller than the orbits. The distance between the supratemporal fossae is half that of the frontal inter-orbital width. The dorsal border of this fossa is surrounded by rugosities, forming an elevation that is more developed in the medial and lateral borders. This condition is similar to *Sebecus* and the peirosaurid *Hamadasuchus*, differing from any other mesoeucrocodyliforms (sensu Benton & Clark 1988 [20]) known to date. The palpebral bones, which are present as anterior and posterior elements in other sebecids (e.g. *Sebecus*, Lumbrera form [4,26]) and specially in “peirosaurids” (e.g. *Lomasuchus*, *Uberahasauchus*, *Montealtosuchus*) [27–29], are not preserved. Even so, the orbit is placed rather laterally, a typical terrestrial sebecid feature, and not laterodorsally as in semi-aquatic crocodyliform morphotypes (e.g., *Stolokrosuchus*, *Lorosuchus* [4,24], and extant species). The frontal is broad and triangular, with a low and smooth longitudinal crest running from the middle part to the posterior portion this bone. A longitudinal frontal crest is a common characteristic for many basal mesoeucrocodylian species, which includes some sebecosuchian taxa (e.g. *Sebecus*; *Zulmasuchus*; *Iberosuchus macrodon*; *Pepesuchus*, *Lorosuchus* [4,16,23,30]). The frontal ornamentation is similar to that on the maxilla, with the wrinkles starting at the frontal longitudinal crest directed to the lateral margins. The jugal is very large and ornamented like most other cranial bones. The posterior ramus is laterally expanded and higher than the anterior one, an unusual feature within sebecosuchians only previously observed in *Bretesuchus* [8]. The ventrolateral margin is concave, a unique feature among basal mesoeucrocodylians. The quadratojugal takes part in the crano-mandibular articulation forming the “double articulation” (sensu Buffetaut 1975 [31]), a feature absent in extant eusuchians but observed in all sebecid species and some other not closely related taxa (e.g. *Trematochampsia*, *Libysocushus*, *Dyrosauridae*). The squamosal shows a developed scupltured dorsal posteriorly pointed lobe (the squamosal posterior process or the squamosal prong [32] that is directed posteriorly and does not

**Figure 4. Sahitisuchus fluminensis gen. et sp. nov. (MCT 1730-R), in left lateral view.** A, photo; B, illustration. For abbreviations see Figure 1. Scale bar: 100 mm. doi:10.1371/journal.pone.0081386.g004

**Figure 5. Sahitisuchus fluminensis gen. et sp. nov. (MCT 1730-R), in occipital view.** A, photo; B, illustration. For abbreviations see Figure 1. Scale bar: 100 mm. doi:10.1371/journal.pone.0081386.g005
form a horn, similar to Hamadasuchus and Lomasuchus [27,32]. Sebecus also shows such a developed process, but differs from Sahitisuchus by a more squared-shape posterior end [23]. The quadrates are massive and mostly unsculptured. The portion of the tympanic cavity formed by the quadrate is not multifenestrated like the one found in protosuchians, notosuchians [33] and baurusuchids (e.g. [34]). It also lacks the oblong concavity, which is characteristic of the Baurusuchidae [34–36] but, like Sebecus, Hamadasuchus and recent species, shows only two openings: the small, anterior preotic siphonial foramen, followed by the larger, oval otic incisure. The ventral portion of the tympanic membrane was supported by a low and sharp semicircular crest. The quadrate distal body extends beyond the occipital limits and bears a well-developed sharp crest that runs from the lateral region of the cranioquadrate passage to the end of this bone. A semi-elliptical shallow concavity in the most distal portion of the quadrate body, just medial to the quadratojugal-quadrate suture and anterior to the cranial-mandibular articulation is very conspicuous in the new species (Figures 2, 5). In ventral view the quadrate exhibits pronounced crests A and A’ [37] for M. adductor mandibularis posterior [38].

Palatal region

The anterior process of the palatine projects over the maxillary palatal shelf with a “U-shaped” anterior margin [39], which extends well forward from the anterior margin of the suborbital fenestrae (Figure 3). The pterygoids are broad wing-shaped elements, similar to those found in Sebecus (MMP 235), being distinct from the broad quadrangular pterygoid of Zulmasuchus, peirosaurids (e.g. Montealtosuchus, Hamadasuchus) and derived eusuchians. The lateral border of the pterygoid flanges are arched and curved inwards similar to Zulmasuchus [9,16]. In Bretesuchus this curvature is even more accentuated than in the latter species [8]. The pterygoid plate is slightly concave, very large and broad. The basicranium is not verticalized as found in Eusuchia but more verticalized than some basal crocodyliform forms (e.g. baurusuchids and sphagesaurids) (Figures 3, 5). The choanae are positioned between the palatine and pterygoid, having a low and laminar choanal septum. The choanal groove (or fossa) is circular as the one of Sebecus and Barinasuchus but comparatively smaller than in these taxa.

Occipital region

The occiput is about four times wider than high, which is partially attributed to crushing of the specimen (Figure 5). On the skull roof, the supraoccipital, this bone is as a relatively small forward pointed triangle which is inserted between the parietals. In

Figure 6. Fourth mandibular tooth from the left side of Sahitisuchus fluminensis gen. et sp. nov. (MCT 1730-R), showing the serrations. A, labial surface; B, detail for apex carina; C, detail for middle carina; D, detail for basal carina. Scale bar in A: 10 mm; B, C and D: 1 mm.
doi:10.1371/journal.pone.0081386.g006

Figure 7. Sahitisuchus fluminensis gen. et sp. nov. (MCT 1730-R) cervical vertebrae. A, right lateral view of axis and third cervical vertebra; B, anterior view, showing the odontoid process. cvt cv3, centrum of third cervical vertebra; di cv3, diapophysis of third cervical vertebra; cvt cv3, postspinal lamina of third cervical vertebra; na cv3, neural arch of third cervical vertebra; ns cv3, neural spine of third cervical vertebra; pa cv3, parapophysis of third cervical vertebra; poz cv3, postzygapophysis of third cervical vertebra; pr cv3, prezygapophysis of third cervical vertebra. Scale bar: 10 mm.
doi:10.1371/journal.pone.0081386.g007
occipital view this bone is relatively large and exhibits a prominent nuchal crest. The latter comprises the insertion point for \textit{M. spinalis capitis} \[40\]. The posttemporal fenestrae are not well preserved due to compression, but the preserved part is very reduced with no postoccipital process. The supraoccipital descending portion is acute and reaches the foramen magnum. However, this seems more the product of the compression than to an autapomorphic feature of the new species. The \textit{exoccipital} has a very distinct mediodorsal process similar to \textit{Ayllusuchus}. This process is sharp and has a semilunate shape, comprising the insertion point for the \textit{M. rectus capitis sublimus} and \textit{M. spinalis capitis}. The \textbf{basioccipital} is trapezoidal and positioned oblique (\textasciitilde45\textdegree) relative to the horizontal plane. This bone possesses a median elevated crest (insertion point for the \textit{M. rectus capitis anterior}). The \textbf{basisphenoid} is short and completely verticalized, being little exposed both in occipital and palatal views. Similar inclination of basisphenoid and basioccipital is also found in some sebecids (e.g. \textit{Zulmasuchus} and \textit{Bretesuchus}) and peirosaurids.

**Mandible**

In ventral view the mandible shows an inverted “Y-shape” (Figures 3, 4). The robust mandibular symphysis is formed by the dentaries and splenials and reaches to opposite the fourth maxillary teeth while the dentary teeth are not visible, occupying about 21\% of the mandibular length. In lateral view the anterior mandible portion is not as high as those of \textit{Bretesuchus} and \textit{baurusuchids}. The \textit{splenial} forms about one-fourth of the mandibular symphysis and medially covers the Meckelian channel as a vertical and thick bone lamina. The \textbf{mandibular lateral fenestrae} is closed, an unusual feature in crocodyliforms and differing from all other sebecosuchian taxa. The \textbf{angular} exhibits a robust well-developed ventrolateral ridge that runs over almost

| Table 1. Measurements in mm of \textit{Sahitisuchus fluminensis} gen. et sp. nov. (MCT 1730-R), adapted from \[25\] \textendash, estimated measurement. |
|-------------------------------------------------|
| 1. greatest width | 179 |
| 2. width of rostrum, posterior | 97 |
| 3. interorbital distance | 60 |
| 4. orbit length | 52.2 |
| 5. skull table width, anterior | 67 |
| 6. skull table length | 96 |
| 7. skull table width, posterior | \textasciitilde143.8 |
| 8. occipital condyle width | 23 |
| 9. occipital condyle height | 15 |
| 10. orbit width | 26.6 |
| 11. choana width | 39 |
| 12. choana length | 35.5 |
| 13. skull roof length | 67 |
| 14. quadrate condyle width | 37.7 |
| 15. supratemporal fossa width | 28.4 |
| 16. supratemporal fossa length | 34.4 |
| 17. palatal fenestra length | \textasciitilde48.6 |
| 18. pterygoid flanges width | \textasciitilde125.5 |
| 19. rostrum width at secondary dental peak | \textasciitilde50.3 |
| 20. rostrum width at notch (or fossa) for 4\textsuperscript{th} mandibular tooth | \textasciitilde35.4 |
| 21. palatine bar width | 38 |
| 22. mandible length | \textasciitilde369 |
| 23. symphysis length | \textasciitilde84.2 |
| 24. retroarticular process length | 44 |
| 25. distance between supratemporal fossa/fenestra | 17 |
| 26. distance between medial borders of supratemporal fossae | 15.3 |
| 27. supratemporal fenestra width | 13.8 |
| 28. supratemporal fenestra length | 22 |
| 29. distance between supratemporal fossa and lateral margin of skull roof (at po–sq suture level) | 21 |
| 30. distance between supratemporal fossa and posterior margin of skull roof | 22 |
| 31. quadrate distal body length | 31.5 |
| 32. laterotemporal fenestra length | \textasciitilde38.6 |
| 33. occiput height (dorsal skull roof surface to occipital condyle) | 38 |
| 34. occiput height (dorsal skull roof surface to medial exoccipital ventral margin) | 54.7 |

\[\text{doi:10.1371/journal.pone.0081386.t001}\]
movements. The fossa, a structure that does not allow palinal-propalinal jaw sebecosuchians, as in baurusuchids. The retroarticular process glenoid fossa, like in other sebecids but unlike some other articular component [38,41]. The insertion point for the components of the retroarticular process, this structure is regarded as the probable this crest is only incipient or poorly developed. With the present below the glenoid fossa (Figure 3A, B). Except for developed ridge with a smooth dorsal and rugose ventral surface is gently convex. The dorsal margin of this bone is arched. A slightly ornamented. In lateral view, the suture with the dentary is inclined ventromedially forming an angle of about 40 “tongue shaped”. Seen from posterior view, the posterior margin margin. The most medial posterior part, formed by the articular, is arched with a concave dorsal articular and the surangular, is arched with a concave dorsal and broad diapophyses, and the length of the third cervical vertebra is subequal compared to the axis.

Discussion and Conclusions

In order to investigate the phylogenetic position of Sahitisuchus fluminensis, we used the data matrix published by Pol et al. 2012 [17], who have considered all well-known sebecid taxa (see Data S1). The analysis was run through TNT, with characters either unordered or ordered and both results show that Sahitisuchus is a member of the Sebecidae (Figure 8). Furthermore, the addition of the new Brazilian taxon collapses the monophyletic genus Sebecus recovered in previous studies [17] and suggests that Barinasuchus occupies a basal position within the Sebecidae relative to Lariosuchus.

The overall crocodyliform record in number of specimens and taxa from Paleocene deposits is rather slim. This low diversity contrasts with the expressive crocodyliform record of the Cretaceous, where a great number of species thrived in a variety of ecological niches, particularly in the Gondwana, such as notosuchians (e.g. Uruguayosuchidae, Sphagesauridae), baurusuchids (e.g. Baurusuchus, Stacitosuchus, Polacanthus), peirosaurids (e.g. Uberabasuchus, Pepesuchus, Hamadasuchus), mahajangasuchids (e.g. Mahajangasuchus and Kaprosuchus), and other taxa whose phyloge-netic position is more controversial [e.g. 44].

Only three crocodyliform lineages are represented either before and after the K-Pg boundary: the marine Dypnoosauridae,

the entire angular length, probably corresponding to the insertion area for the strongest component of the mandibular adductory musculature (M. adductor mandibulae internus pterygoideus ventralis [38]).

The surangular takes part in the glenoid fossa, is stout and slightly ornamented. In lateral view, the suture with the dentary is gently convex. The dorsal margin of this bone is arched. A developed ridge with a smooth dorsal and rugose ventral surface is present below the glenoid fossa (Figure 3A, B). Except for Brevesuchus, in all other sebecosuchids where this region is preserved this crest is only incipient or poorly developed. With the retroarticular process, this structure is regarded as the probable insertion point for the components of the M. depressor mandibulae component [38,41]. The articular forms about 60% of the glenoid fossa, like in other sebecids but unlike some other sebecosuchians, as in baurusuchids. The retroarticular process shows an elevated lateromedially crest just posterior to the glenoid fossa, a structure that does not allow palinal-propalinal jaw movements. The retroarticular process, formed by the articular and the surangular, is arched with a concave dorsal margin. The most medial posterior part, formed by the articular, is “tongue shaped”. Seen from posterior view, the posterior margin is inclined ventromedially forming an angle of about 40° relative the horizontal plane. A blunt crest runs longitudinally in the articular portion of this process. The retroarticular foramen acerenum is small and opens close to the medial margin of the retroarticular process, right after the glenoid fossa.

Dentition

The premaxillary teeth are not preserved but at least twelve maxillary teeth must have been present (Figures 4, 6). Due to the fact that the upper and lower jaws are occluded, most of the mandibular teeth are not visible.

The new species has the crocodyliform plesiomorphic pattern of occlusion [3], with the hypertrophied dentary caniniform exposed laterally, occluding in the premaxillary-maxillary fossa, and the following maxillary teeth occluding buccally relative to the mandibular tooth row. The upper dentition is heterodont with three morphological arrangements, all showing serrated carinae formed by true denticles (sensu Langston 1975 [42]) (Figure 6). The first three maxillary teeth are ziphodont, curved posteriorly with pointed and buccolingually compressed crowns. The second dental morphotype is formed by the following two (perhaps three) teeth that are lanceolate and bear straight (i.e., not posteriorly curved) crowns. They are followed by progressively shorter teeth with blunt apices and a marked constriction between root and crown. The large caniniform tooth shows about 3–3.5 denticles per mm (Figure 6).

Cervical elements

Several of the most anterior cervical elements such as the pro-atlas, intercentrum and odontoid process are described for first time in Sebecidae (Figures 3, 7). The pro-atlas was displaced over the left pterygoid flange. It is a small and laminar V-shaped bone with a low dorsal crest. Compared to modern crocodylians, this bone is rather conservative differing mainly by being narrower (Figure 3). The intercentrum, the only part identifiable of the atlas, was also displaced, being preserved over the left suborbital fenestra. This bone is robust, not laminar, with two blunt posteriorly directed processes for the first cervical ribs. The axis is preserved associated with a well-developed odontoid process that is similar to the one found in recent taxa by being massive and showing on each side blunt anterior tuberous processes (Figure 7). In the new species the anterior region is vertical and lacks the small medial processes found in at least some recent taxa. Furthermore, the odontoid process is fused with the axis with no visible suture indicating that this is most likely a very old individual [43]. The axis is well developed with a low, blade-like neural spine. The third cervical vertebra is amphicoelous, with a tall spike-like neural spine, inclined posteriorly, with a postspinal lamina that is bifurcated at the base (Figure 7). As in Sebecus (the only other sebecid where this part of the skeleton was described [17]), the diapophysis is divided by the neurocentral suture and in lateral view, the centrum shows a mediolateral constriction and a trapezoidal shape, with anterior and posterior articulations inclined anteriorly. Among the differences with Sebecus, Sahitisuchus has more robust and broader diapophyses, and the length of the third cervical centrum is subequal compared to the axis.

Table 2. Sahitisuchus fluminensis gen. et sp. nov. (MCT 1730-R) teeth measurements in mm.

| Right tooth row | Left tooth row |
|-----------------|----------------|
| tooth | fabl | tch | tooth | fabl | tch |
| m1   | 4.8  | 14.8 | m1   | 10.9 | 6   |
| m2   | 5.2  | 9.2  | m2   | 14   | 7.5 |
| m3   | 31.5 | 11.7 | m3   | 28.7 | 15.8 |
| m4   | 11.7 | 5.8  | m4   | 10   | 6.4 |
| lmt  | 6.4  | 6.1  | m5   | 8.2  | 5.7 |
| 1std (d 4 ?) | ~26.2 | ~15.6 | 6thm   | – | 9.3 |
| 2nd  | 14.8 | 7.7  | 7thm  | 6.14 | 6   |
| 3rd  | 8.6  | 5    | 8thm  | 6.5  | 7.2 |
| 4th  | –    | 6.6  | 9thm  | –    | 5.7 |
| 5th  | 10thm | 6.4  | 6.1  | 9thm |
| 1std (d 4 ?) s | ~12.8 | 7.1  | | | |

1std (d 4 ?), first exposed dentary tooth of the right side; 1std (d 4 ?) s, first exposed replacement dentary tooth of the left side; d, dentary tooth; fabl, fore-after basal length; lmt, last exposed maxillary tooth; m, maxillary tooth; tch, tooth crown height; -, lack information; ~, estimated measurement.

doi:10.1371/journal.pone.0081386.t002
particularly abundant in coastal deposits of Africa [45,46], the semi-aquatic Crocodylia, recovered especially by alligatoroids from North and South America [15,47–50]; and the terrestrial sebecosuchians (e.g. [17]). Dyrosaurids are very specialized and became quite diversified after the K-Pg boundary, becoming along with sharks the main marine predators after the demise of mosasaurs [6]. Although the Alligatoroidea were already present in the Late Cretaceous this group only diversified after the K-Pg biotic crises (e.g. [39,49]), contrary to what happened with the sebecosuchians that became less diverse (with baurusuchids restricted to Upper Cretaceous e.g. [34]).

So far, the only Paleocene deposit where members of the Alligatoroidea (Eocaiman itaboraiensis [15]) and Sebecosuchia (represented by Sahitisuchus) were recovered is the São José de Itaboraí Basin. Having its origin related to the separation of South America and Africa, resulting in the opening of the South Atlantic Ocean [51], this tectonic feature consists of a small half-graben with a NE-SW major axis of 1.400 m and a sedimentary sequence that reaches a maximum thickness of 125 m [52]. The main fossils described so far are mammals that record one of the earliest phases of the mammalian radiation in South America after the K-Pg biotic crisis (e.g. [53]). The inferred age of the Itaboraí Basin based on the mammalian fauna has been the matter of a recent debate [21,53–55]. Despite this uncertainty, the new crocodyliform is part of the so-called S2 paleofauna, whose age (Itaboraian SALMA [55]) is considered middle Upper Paleocene varying in absolute terms between 61.8 million to 58.5 million years [12] or 58.5 million to 56.5 million years [22].

The co-occurrence of a remnant of the pre-K-Pg sebecosuchian and a post-K-Pg alligatoroid crocodyliform taxon, here represented by Sahitisuchus and Eocaiman [15], respectively, in the Paleocene deposits of the Itaboraí Basin is quite unusual and somewhat surprising. The taphonomic history of those specimens, as of other fossils found in this basin, has been difficult to retrieve, particularly due to the fact that all material was recovered from fissures and not detailed information about their collecting has been recorded. This raises the valid question if all fossils were synchronous [e.g., 56–57]. In the lack of other information, some authors have used the color of the specimens to establish if they came from the same or distinct fissures that stands as a proxy for being regarded synchronous [56].

Regarding the crocodyliforms, it is clear that the sebecid and the alligatoroid species came from distinct environments (terrestrial and semi-aquatic, respectively) and represent animals that lived around a freshwater lake before becoming preserved. Among the specimens attributed to Eocaiman, several show distinct colors suggesting that they come from distinct fissures [15]. The material of Sahitisuchus fluminensis is preserved in a greyish colored limestone, similar to some of the Eocaiman material. Furthermore, despite the questions about the correct absolute age, it has been proposed that the calcareous deposits of the São José de Itaboraí Basin were formed in a time span of 2 million years [37–58] or less. Therefore, we can conclude that Sahitisuchus and Eocaiman were either set apart for a comparatively short geological timespan or most likely co-occurred, the last hypothesis favored here.

One possible scenario that could explain the co-occurrence of Sahitisuchus and Eocaiman is that, right after the Cretaceous-Paleogene biotic crisis, only the less specialized crocodyliforms survived (e.g. [59]), except for the marine dyrosaurids that appear not to have been negatively affected by this event (e.g. [6]).

Regarding sebecosuchians, this appears to be correct since the Cretaceous forms show high skulls and a marked specialization in the dentition that is quite reduced. The Cretaceous taxa Baurusuchus and Stratiotosuchus, for example, show only five maxillary teeth opposed to the 10 in the Paleogene Lurosuchus, Biterosuchus and Zalmoxes, and 12 in Sahitisuchus. Furthermore, Paleocene sebecosuchians represented only by the Sebecidae show the posterior teeth blunt and not specialized as in the Cretaceous sebecosuchians. It is conceivable that the Paleocene sebecosuchians adopted a mixture of semi-aquatic and terrestrial lifestyles and therefore might have at least partially shared the same environments as Paleocene alligatoroids. After the Eocene, sebecosuchians became again more specialized, developing a higher and laterally compressed rostrum as observed in the Eocene Sebecus and the Upper Miocene Langstonia. They further show a trend to reduce dentition (e.g. Sebecus exhibiting nine maxillary teeth), although not approaching the observed in the Cretaceous baurusuchid sebecosuchians.

The unexpected result in the phylogenetic study presented here with the addition of Sahitisuchus to the data matrix published by Pol et al. [17], is the basal position of the high-mounted Baurusuchus. Recovered from Miocene deposits, this very large sebecid is known from the anterior portion of the rostrum only [9]. If its phylogenetic position is correct, this species indicates the presence of a yet another independent sebecid lineage that sometime after the K-Pg biotic crisis developed accentuated oreinirostry (sensu [60]) independently from other sebecids, suggesting a more complex history of the post-K-Pg crocodyliform radiation.

Supporting Information

Figure S1 Topology resulted by heuristic analysis of unordered characters states. Bootstrap values above the lines (branches), at left and no-italic; Jackknife values above lines (branches), at right and italic; Bremer decay below the lines (branches). Data matrix from Pol et al., (2012) [17] with Sahitisuchus fluminensis added. (JPG)

Figure S2 Topology resulted by heuristic analysis of third seven ordered characters states. Bootstrap values above the lines (branches), at left and no-italic; Jackknife values above lines (branches), at right and italic; Bremer decay below the lines (branches). Data matrix from Pol et al., (2012) [17] with Sahitisuchus fluminensis added. (JPG)

Data S1 Phylogenetic Analyses. (DOC)

Acknowledgments

We thank Jessica Pontes da Silva [MN/UFRJ] for preparing the specimen, Orlando N. Grillo [MN/UFRJ] for helping with the pictures, Carla W. Gabriel [Microscopy Laboratory technician DEGEO/CCMN/UFRJ] for the microscopic images, and Lilian P. Bergqvist [DEGEO/CCMN/UFRJ] for information about the São José de Itaboraí Basin. We also would like to thank Chris Brochu (University of Iowa, EAU), James Clark (Washington University, EAU) and an unknown reviewer for comments and suggestions on that improved this contribution.
Author Contributions
Conceived and designed the experiments: AWAK AEPP DAC. Performed the experiments: AWAK AEPP DAC. Analyzed the data: AWAK AEPP DAC. Contributed reagents/materials/analysis tools: AWAK AEPP DAC. Wrote the paper: AWAK AEPP DAC.

References
1. Hekkala E, Shirley MH, Amato G, Austin JD, Charter S, et al. (2011). An ancient icon reveals new mysteries: mummy DNA resurrects a cryptic species within the Nile crocodile. Molecular Ecology 20: 4199–4213. (doi:10.1111/j.1365-294X.2011.05245.x).
2. Brochu CA (2001). Crocodilian snouts in space and time: phylogenetic approaches toward adaptive radiation. American Zoologist 41: 564–585.
3. Brochu CA (2003). Phylogenetic approaches toward crocodylian history. Annual Review of Earth and Planetary Sciences 31: 357–397.
4. A D, Powell JE (2011). A new sebecid mesoeucrocodylian from the Rio Loro Formation (Paleocene) of north-western Argentina. Zoological Journal of the Linnean Society 163: 7–36.
5. Gasparini Z (1996). Biogeographic Evolution of the American Crocodilians, Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Palaeontologie 30: 159–184.
6. Barbosa JA, Kellner AWA, Viana MSS (2008). New dyrosaurid crocodylomorph and evidences for faunal turnover at the K-P transition in Brazil. Proceedings of The Royal Society B, 275: 1385–1391.
7. Simpson GG (1937). New reptiles from the Eocene of South America. American Museum Novitates 927: 1–3.
8. Gasparini Z, Fernandez M, Powell J (1993). New Tertiary Sebecosuchians (Crocodylomorpha) from South America: Phylogenetic Implications. Historical Biology 7: 1–19.
9. Paolillo A, Linares O (2007). Nuevos crocodilos sebecosuchia del cenozoico suramericano: Mesocrocodylia: Paleobiología Neotropical 3: 1–25.
10. Klein VC, Bergqvist LP (2002). Excursão à Bacia de São José de Itaboraí, Rio de Janeiro, Brazil. Contribuição para a geologia e sedimentologia da Bacia do São José de Itaboraí, Brasil. Bulletin, II Congresso Pan-Americano de Engenharia de Minas e Geologia, Rio de Janeiro 3: 149–173.
11. Paula-Couto C (1953). A Bacia Calcarea de Itaboraí e a tectônica da costa Sudeste do Brasil. Notas Preliminares e Estudos da Divisão de Geologia e Mineralogia do DNPM, Rio de Janeiro 75: 1–17.
12. Bergqvist LP, Moreira AL, Pinto DR (2005). Bacia de São José de Itaboraí, Rio de Janeiro, Brazil: lithostratigraphy and biostratigraphy. Acta Geológica, 33: 291–314.
13. Price LI, Paula-Couto C (1946). Vertebrados Terrestres do Eoceno na Bacia Carbonífera de Itaboraí, Brasil. Bulletin, II Congresso Pan-Americano de Engenharia de Minas e Geologia, Rio de Janeiro: 3: 149–173.
14. Kellner AWA, Campos DA (1999). Vertebrate paleontology in Brazil: a review. Palaeontology 42: 953–957.
15. Buffetaut E, Marshall LG (1991). A new crocodylian, Allognathosuchus montealtosuchus, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous of Brazil and the Phylogeny of Pythosuchids. Plos One 6. (e21916). doi:10.1371/journal.pone.0021916.
16. Iordansky NN (1973). The skull of the Crocodylia. In: Gans C ed. Biology of the Reptilia, Academic Press, London and New York 4: pp. 201–262.
17. Brochu CA (1999). Phylogenetics, Taxonomy, and Historical Biogeography of Alligatoridae. Journal of Vertebrate Paleontology 19: 9–100.
18. Chaisson RB (1982). Laboratory Anatomy of the Alligator: The Alligator University of Arizona, WM.C. Brown Company Publishers, pp. 1–36.
19. Iordansky NN (2000). Jaw Muscles Of The Crocodiles: Structure, Synonymy, and some implications on Homology and Functions. Russian Journal of Morphology and Phylogeny 4: 539–569.
20. Larsson HCE, Sues H-D (2007). Cranial Osteology and Phylogenetic Relationships of Hesperosuchus (Crocodyliformes: Meso-Crocodylia) From The Cretaceous of Morocco. Zoological Journal of the Linnean Society 149: 533–567.
21. Buffetaut E (1975). Sur l’articulation entre le quadratojugal et le surangulaire de certains Crocodiliens fossiles. Comptes Rendus Acad Sc Paris, D 280: 2741–2743.
22. Larsson HCE, Sues H-D (2007). Cranial Osteology and Phylogenetic Relationships of Hesperosuchus (Crocodyliformes: Meso-Crocodylia) From The Cretaceous of Morocco. Zoological Journal of the Linnean Society 149: 533–567.
23. Hecth MK, Tanissto SF (1983). On the cranial morphology of Protosuchia, Norosuchia and Eusuchia. Konstruktionsmorphology 132: 657–669.
24. Montélétrio FC, Larson HCE, Langer MC (2011). A New Bauursuchid (Crocodyliformes, Meso-Crocodylia) from the Late Cretaceous of Brazil and the Phylogeny of Pythosuchidae. Plos One 6. (e21916). doi:10.1371/journal.pone.0021916.
25. Paula-Couto C (1953). A Bacia Calcarea de Itaboraí, Brasil. Bulletin, II Congresso Pan-Americano de Engenharia de Minas e Geologia, Rio de Janeiro: 3: 149–173.
26. Barros JA, Kellner AWA, Viana MSS (2008). New dyrosaurid crocodylomorph and evidences for faunal turnover at the K-P transition in Brazil. Proceedings of The Royal Society B, 275: 1385–1391.
27. Pol D, Leardi JM, Lecuona A, Krause M (2012). Postcranial anatomy of Allophyes nov.sp. of the early Cenozoic of Brazil: Phylogenetic Implications. Historical Biology 35: 357–397.
28. Carvalho IS, Ribeiro LCB, Avilla L (2004). Stratiotosuchus maxhechti nov. sp., a new peirosaurid crocodile (Mesoeucrocodylia) From the Late Cretaceous of Brazil and the Phylogeny of Pythosuchidae. Plos One 6. (e21916). doi:10.1371/journal.pone.0021916.
29. Buffetaut E (1975). Sur l’articulation entre le quadratojugal et le surangulaire de certains Crocodiliens fossiles. Comptes Rendus Acad Sc Paris, D 280: 2741–2743.
30. Larsson HCE, Sues H-D (2007). Cranial Osteology and Phylogenetic Relationships of Hesperosuchus (Crocodyliformes: Meso-Crocodylia) From The Cretaceous of Morocco. Zoological Journal of the Linnean Society 149: 533–567.
31. Hecht MK, Tansissto SF (1983). On the cranial morphology of Protosuchia, Norosuchia and Eusuchia. Konstruktionsmorphology 132: 657–669.
32. Montélétrio FC, Larson HCE, Langer MC (2011). A New Bauursuchid (Crocodyliformes, Meso-Crocodylia) from the Late Cretaceous of Brazil and the Phylogeny of Pythosuchidae. Plos One 6. (e21916). doi:10.1371/journal.pone.0021916.
33. Buffetaut E (1975). Sur l’articulation entre le quadratojugal et le surangulaire de certains Crocodiliens fossiles. Comptes Rendus Acad Sc Paris, D 280: 2741–2743.
53. Muizon C, Brito IM (1993). Le Basin calcaire de São José de Itaborai (Rio de Janeiro, Brésil) ses relations fauniques avec le site de Tiupampa (Cochabamba, Bolivie). Annales Paléontologie 79: 233–269.

54. Gelfo JN, Goin FJ, Woodburne MO, Muizon C (2009). Biochronological relationships of the earliest south american paleocene mammals faunas. Palaeontology 52: 251–269.

55. Paula-Couto C (1952). Fossil mammals from the beginning of the Cenozoic in Brasil. Marsupialia: Polydolopidae and Borhyaenidae. American Museum Novitates 1539: 1–27.

56. Bergqvist LP, Almeida ER, Araújo-Júnior H (2011). Tafonomia da assembleia fossilífera de mamíferos da “Fenda 1968”, Bacia de São José de Itaborai, Estado do Rio de Janeiro, Brasil. Revista Brasileira de Paleontologia 14(1):75–86.

57. Rage J-C (1998). Fossil snakes from the Paleocene of São José de Itaborai, Brasil. Part I. Madtsoiidae, Aniliidae. Paleovertebrata 27: 109–104.

58. Marshall LG, Sempere T, Butler RF (1997). Chronostratigraphy of the mammal-bearing Paleocene of South America. Journal of South America Earth Sciences 10(1): 49–70.

59. Buffetaut E (1990).Vertebrate extinctions and survival across the Cretaceous–Tertiary boundary. Tectonophysics 171: 337–345.

60. Bushey AB III (1995). The structural consequences of skull flattening in crocodylians. In: Thomason J, ed. Functional morphology in vertebrate paleontology. London: Cambridge University Press. pp 171–192.