A new genus of pipimorph frog (Anura) from the Early Cretaceous Crato Formation (Aptian) and the evolution of South American tongueless frogs

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ABSTRACT

Pipimorpha is a clade of tongueless anurans with a wide fossil record. Furthermore, the oldest South American fossils come from the Late Cretaceous (Cenomanian) of Patagonia, Argentina. The aim of the present contribution is to describe a new genus and species of Pipimorpha from the Crato Formation (Aptian, Early Cretaceous), Araripe Basin, Brazil. The new specimen consists of a nearly complete skeleton that shows several anatomical similarities with other fossils from South America. Phylogenetic analysis resulted in the nesting of the new taxon within a previously unrecognized endemic South American clade. Further, some traditional groupings within Pipimorpha were not recognized. The new phylogenetic analysis reinforces previous biogeographical hypotheses sustaining dispersal of pipimorph between Africa and South America through an island chain or continental bridge across the Atlantic Ocean.

1. Introduction

Pipimorphs are fully aquatic frogs that are currently represented by five living genera distributed in tropical South America and sub-Saharan Africa (Cannatella, 2015; Gomez, 2016). The fossil record of pipimorphs is extensive, specially in South America, where it is represented by several genera and species ranging from the Late Cretaceous (Báez, 1987; Gomez, 2016) to the Pleistocene (Báez et al., 2008). The oldest certain record of the clade belongs to the Late Cretaceous of Patagonia (Cenomanian-Turonian) (Báez et al., 2000).

The Crato Formation (Early Cretaceous, Aptian) probably represents the most diverse biota known from the Early Cretaceous of South America (Martill et al., 2007a,b). It comprises a large number of plants and animals, including dinosaurs, birds, lepidosaurs, fishes, and anurans (Martill et al., 2007a,b). Among the latter, Leal and Brito (2006) were the first authors to describe in detail fossil frogs from the Crato Formation. They coined the genus and species *Arariphrynus placidoi* on the basis of several nearly complete specimens that they referred to the neobatrachian clade Leptodactylidae. Later, Leal et al. (2007) illustrated new material from the Crato Formation, including the poorly preserved skeleton of a possible pipoid. More recently, Báez et al. (2009) reviewed available material and conclude that *Arariphrynus* was a composite, and included several taxa belonging to disparate groups within Neobatrachia. Further, Báez et al. (2009) reported on an incomplete specimen that was not identified with certainty and was regarded as an indeterminate anuran with probably pipimorph affinities (Báez et al., 2009).

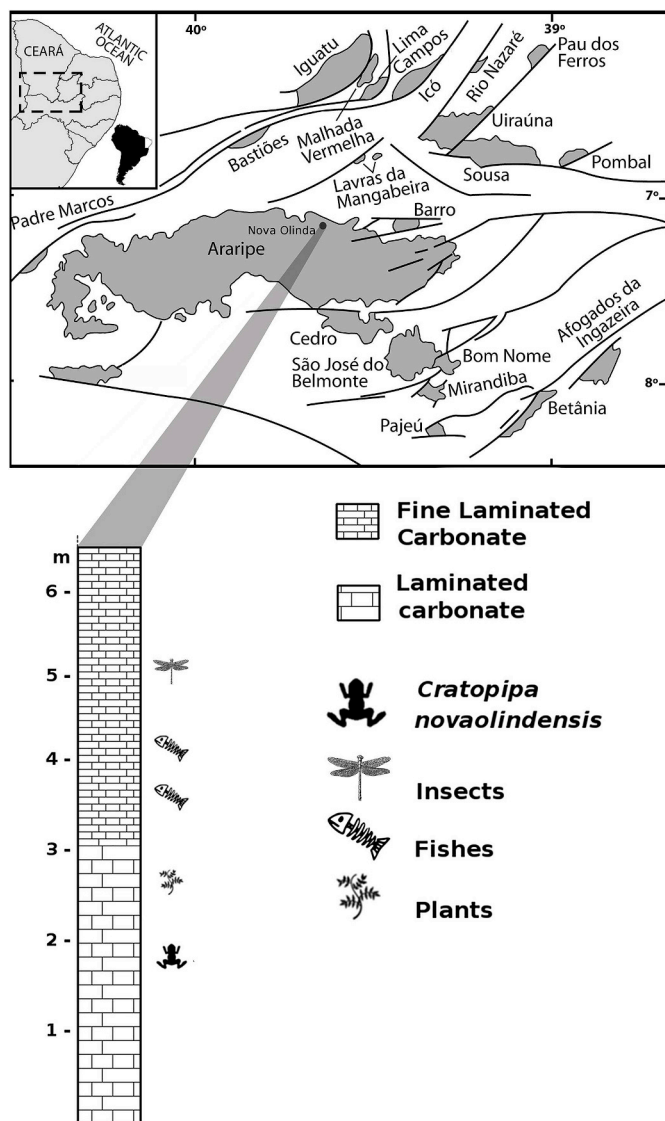The aim of the present contribution is to describe a nearly complete

Fig. 1. Location map of the Araripe Basin in the context of the Cretaceous Brazilian Northeastern intracratonic basins and stratigraphical profile of the location where the fossil was collected. Pedra Branca Mine, Nova Olinda County, Brazil (7° 6′ 51.9″ S and 39° 41′ 46.9″ W).

skeleton of a new anuran genus and species from the Crato Formation (Fig. 1). This new specimen is very well preserved, and its skeletal anatomy indicates that it belongs to Pipimorpha. This record constitutes the oldest known for the clade in South America and has a great importance for pipimorph biogeography and evolution.

2. Materials and methods

For descriptive purposes we follow the anatomical terminology provided by Báez and Púgener (2003), whereas tarsal and carpal morphology follows Báez et al. (2009). In order to assess the phylogenetic relationships of the new taxon among pipimorphs we relied on the osteological characters used by Cannatella and Trueb (1988), Báez and Trueb (1997), and Gómez (2016). We followed the taxonomic nomenclature employed by Frost et al. (2006) and Frost (2015), as modified by Gómez (2016).

A phylogenetic analysis was conducted with the purpose of assessing the phylogenetic relationships of the new taxon with other pipimorphs. The data matrix is based on the extensive analysis published by Gómez (2016). Characters 166–176 were added, based on personal observations (Appendix A). The coding of character 39 was modified and state 1 was split into two different states (Appendix A). We added a state 2 to character 99 (Appendix A). Finally, "*Shelania*" *laurenti* (Báez and Púgener, 1998) and "*Xenopus*" *romeri* (Estes, 1975) are fragmentary and poorly informative, represented by non-associated specimens, and thus, resulted as wildcard taxa. In this way, following Aranciaga et al. (2018) they were excluded from the phylogenetic analysis. The modifications resulted in a data matrix consisting of 176 characters scored for 35 taxa (Appendix B) (see Aranciaga et al., 2018).

The phylogenetic analysis was performed using TNT 1.1 (Goloboff et al., 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1000 pseudoreplicates of WAG + TBR search strategy, with 10 random addition sequences after each search and 100 trees were saved at each replicate.

3. Geological context

The Araripe Basin is a Northeastern Brazilian interior basin $(12,200 \text{ km}^2)$ related to the first Neocomian tectonic phase of the South Atlantic opening (Matos, 1992). This is a hinterland basin, developed during a phase of mechanical subsidence in a rift system (Matos, 1992). The tectonism resulted in two depositional areas –Feira Nova and Cariri– bordered by transfer faults (Carvalho et al., 2015a).

The lithostratigraphy of the Araripe Basin has been discussed by many authors (Beurlen, 1962, 1971; Hashimoto et al., 1987; Cavalcanti and Viana, 1992; Ponte, 1992; Martill, 1993; Martill and Wilby, 1993; Viana and Neumann, 1999; Assine, 2007). This basin was mainly filled, with clastic and chemical rocks deposited in alluvial fans, shallow lakes, and braided and meandering rivers (Carvalho, 2000; Carvalho and Melo, 2012). During the late Aptian, the main environments were anoxic and saline lakes, in which carbonates and sulfates were deposited (Crato and Santana Formations). The new fossil was collected in the Crato Formation (previously considered as Crato Member of Santana Formation). Rios-Netto et al. (2012) used a biostratigraphical framework based on palynological analyses to assign this sedimentary succession to the late Aptian (109–113 My).

The Crato Formation is considered a fossil Lagerstätte, containing probably one of the most well-known terrestrial flora and fauna from the Aptian time, due to the large amount and quality of its fossils (Depeche et al., 1990. Pons et al., 1990; Maisey, 1991; Viana and Neumann, 1999; Carvalho and Santos, 2005; Arai et al., 2004; Martill et al., 2007a; Carvalho et al., 2012). It comprises a 60-m-thick succession of metric-scale laminated carbonate units interlayered with equally thick successions of green shales and fine-to-coarse sandstones. Halite pseudomorphs in distinct carbonate levels suggests fluctuating salinity conditions (Silva and Neumann, 2003; Heimhofer et al., 2010; Martill et al., 2007b). The laminated carbonatic strata were deposited during a hot and arid climate. South America and Africa together formed a single large continental block resulting in low humidity environments (Carvalho, 2000, 2004; Carvalho and Pedrão, 1998). This stress environment is favorable for the bloom of algal mats and microbial communities in the photic zones of a shallow lake (Catto et al., 2016). In this regard, experimental taphonomy with vertebrates conducted by Iniesto et al. (2013, 2015, 2016, 2017) showed the interaction between microbial activity and the vertebrate carcasses, allowed for exceptionally preserved fossils, with complete articulation and preservation of soft tissues. These authors have analyzed the carcasses decay and preservation and the metabolic changes exerted by the microbial mats.

4. Systematic palaeontology

Anura Rafinesque, 1815
Pipoidea Fitzinger, 1843
Pipimorpha Ford and Cannatella, 1993
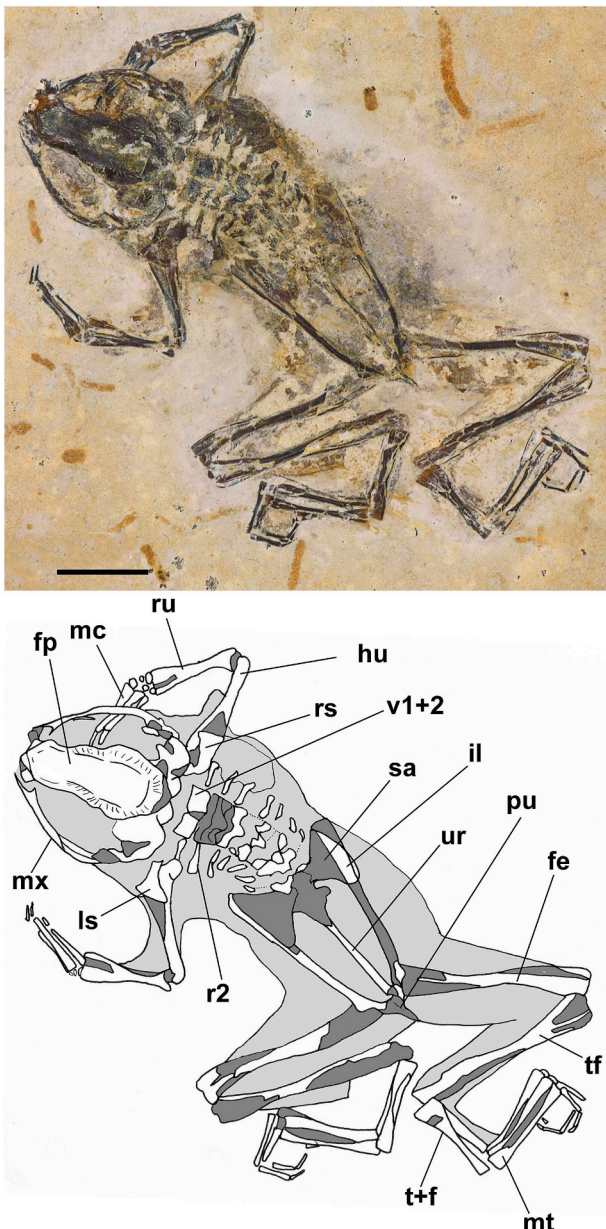*Cratopipa novaolindensis* nov. gen. et sp. (Fig. 2)

Fig. 2. Holotype specimen of *Cratopipa novaolindensis* nov. gen. et sp. (UFRJ-DG 05 A). Abbreviations: fe, femur; fp, frontoparietal; hu, humerus; il, ilium; ls, left scapula; mc, metacarpal; mx, maxilla; pu, pubis; r2, second rib pertaining to presacral vertebrae 2; rs, right scapula; ru, radioulna; sa, sacrum; mt, metatarsal; t + f, tibiale + fibulare; tf, tibiofibula; ur, urostyle; v1 + 2, fused presacrals 1 and 2. Shaded in dark grey: damaged areas of skeleton; Shaded in light grey: body outline. Scale bar: 5 mm.

Diagnosis. Small pipimorph frog showing the following unique combination of characters (autapomorphies marked by an asterisk*): 1- thickened and longitudinally concave frontoparietal, with dorsally vaulted and strongly ornamented orbital margins*; 2- posterior end of frontoparietal with expanded flanges that overlap the braincase; 3- posterior end of maxilla contacts the squamosal; 4- proximal half of humerus anteroposteriorly thickened*; and 5- notably short tibiale + fibulare that do not reach half the length of the tibiofibula.

Derivation of the name. *Crato*, from Crato Formation, the lithostratigraphic unit in which the holotype specimen was found; *Pipa*, the type genus of the Pipidae family. The specific epithet *novaolindensis* refers to the county of Nova Olinda, Ceará State, Brazil, the site where the fossil was discovered.

Bone	length	width
fp	7.07	2.37
mx	7.22	0.42
ap	?	?
pmx	0.36	?
na	0.43	0.59
mc	2.84	0.14
ls	2.99	1.92
rs	3.01	2.00
ru	5.69	1.79
hu	7.71	0.89
pc	7.04?	3.59
v1 + 2	1.37	1.47
r2	1.94	0.27
occ	1.3	0.92
il	12.5	0.58
sa	4.41	2.92
ur	7.05	0.31
pu	2.08	0.74
fe	11.91	0.38
tf	12.9	0.83
t + f	6.18	1.59
m + t	6.92	0.50

Locality and horizon. The type specimen comes from Pedra Branca Mine, Nova Olinda County, Ceará State, Brazil (7° 6′ 51.9” S and 39° 41' 46.9” W; Fig. 1). The specimen was found in strata belonging to the Crato Formation, Early Cretaceous (Aptian).

Holotype. UFRJ-DG 05 A (Universidade Federal do Rio de Janeiro, Departmento de Geologia collection), a nearly complete and articulated skeleton, including impressions of soft tissue and skin.

4.1. Description

The specimen is represented by a nearly complete and articulated skeleton (snout-vent length of the frog is about 35 mm, Table 1). Because of strong dorsoventral compression, several anatomical details are not discernible, and morphology of the ventral side of the skeleton remains unknown. Most of the pectoral girdle and details of several skull bones are not preserved or are badly damaged. The skull and postcranial skeleton are well-ossified.

The skull (Fig. 3) is slightly longer than wide. The major width of the skull is at level of the mid-length of the frontoparietal, due to strong lateral convexity of maxillae. The preorbital region of the skull is short, representing approximately one fifth of the total skull length.

Nasals and premaxillae are very poorly preserved. Nasals are relatively short and wide, and are not fused along the midline. Anterior processes of the nasals appear to be short.

The frontoparietal is the largest element of the skull. It is azygous and well-ossified and forms most of the skull roof. The anterior half of the bone is transversely narrower than the posterior half. It is longitudinally concave, and the orbital margins are delimited by thickened parasagittal crests that are dorsally vaulted and ornamented by feebly developed ridges and grooves.

The anterior margin of the frontoparietal is acute, resulting in a subtriangular contour. Posteriorly the frontoparietal overlaps the otic capsules. The lateral flanges of the frontoparietal at its posterior half are well-ornamented, and strongly laterally deflected, covering a large part of the medial margin of the otic capsules. Orbital margins of the
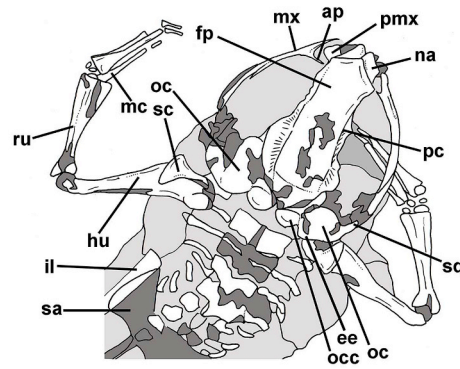
Fig. 3. Detail of skull and anterior portion of the body of *Cratopipa novaolindensis* nov. gen. et sp. Abbreviations: ap, antorbital process of maxilla; ee, epiotic eminence; fp, frontoparietal; hu, humerus; il, ilium; mc, metacarpal; mx, maxilla; na, nasal; oc, otic capsule; ooc, occipital condyle; pc, prasagittal crest; pmx, premaxilla; ru, radioulna; sa, sacrum; sc, scapula; sq, squamosal. Shaded in dark grey: damaged areas of skeleton; Shaded in light grey: body outline. Scale bar: 5 mm.

frontoparietal are sinuous, with a concave anterior half, that is separated from the posterior one by strong but anteroposteriorly short convex edge. A pineal foramen is not evident.

Most of the braincase and palate are not exposed, and thus, anatomical details are not available. Prootic and exoccipitals appear to be fused to one another, forming the otic capsules. The anterior margin of the capsules indicates that each one was notably transversely narrower than the frontoparietal. A partial epiotic eminence has been preserved on the right otic capsule, indicating that this structure was thickened and relatively well-developed. The anterior margin of each capsule is obliquely oriented with respect to the main skull axis. The posterior margin of the capsules is notably convex, and extends posteriorly to the level of the occipital condyles. In spite of being poorly preserved, the foramen magnum was probably not completely encircled by bone (the exoccipitals appear not to be fused to one another).

The premaxillae are highly fragmentary and do not allow recognition of main anatomical details. The maxillae are relatively robust and show a strongly convex lateral margin, especially at their mid-length. The anterior end of the maxillae have a very narrow and acuminate process that arises from the pars facialis and overlaps most of the premaxillae. The pars palatina is strongly reduced, and is difficult to discern the distinction between the pars facialis and pars palatina. The maxilla appears to be edentulous. At the anterior margin of the orbit the maxilla bears a very acute and well-developed antorbital process. Posterior to the antorbital process the maxilla appears to be more robust and the pars palatina is more expanded than in the anterior half of the bone. The posterior end of the maxilla contacts the squamosal.

The vertebral column is comprised of 8 presacral vertebrae (of which only 7 discrete elements are discernible due to fusion of first and second presacrals), the sacrum, and urostyle (Fig. 4). Presacral

vertebrae are subequal in size and shape, but poor preservation precludes the discernment of several anatomical details. The neural arches are relatively simple and imbricate. The atlas is fused to presacral II as indicated by the presence of well-developed transverse processes. The anterior margin of the lamina formed by the neural arches of this complex is nearly straight. The neural spine appears to be restricted to the posterior margin of the neural arch. This vertebral complex is relatively more robust and anteroposteriorly thicker than other presacral elements. Neural arches of presacral vertebrae lack ornamentation with the exception of a single longitudinal ridge running subparallel to the neural spine.

Transverse processes corresponding to presacrals V to VIII are shortened. Their distal ends are relatively robust. The transverse process corresponding to presacral V is laterally oriented, whereas those corresponding to presacrals VI-VIII are anteriorly tilted.

The presacrals II-IV have fused ribs. The first rib is slightly anterolaterally oriented, and gradually expands towards the distal end of the bone. Second and third ribs are posterolaterally oriented.

The sacrum and urostyle are fused, forming a sacro-urostyle complex. This complex shows widely expanded diapophyses with nearly straight lateral margins. The posterior margin of the sacral diapophyses is strongly concave, especially at its base. There are no signs of webs of bone connecting the urostyle and sacral diapophyses. The poor preservation of the sacrum precludes a more detailed description of the element. The urostyle is poorly preserved. It is relatively short, and the length of the shaft is approximately one and a half that of the anteroposterior length of the sacral diapophyses. It lacks any sign of transverse processes.

The pectoral girdle is very poorly known. Only the distal end of both scapulae has been preserved. This element is distally expanded and shows a weakly concave anterior margin and a strongly concave posterior one. The dorsal surface of the element appears to be gently concave.

The forelimbs are poorly preserved and distorted by taphonomical processes. In lateral view the humerus is very robust, and it has a strongly anteroposteriorly expanded proximal end. The deltoid crest is very prominent and forms a deep lamina. The radioulna is robust and stout, being only slightly shorter than the humerus. The proximal end shows a strongly concave articular surface for the humerus and a proximally expanded and robust olecranon process. The distal end is strongly anteroposteriorly expanded.

The carpals are poorly exposed and distorted, and thus, detailed interpretation is difficult. The radial and intermedium + ulnar elements are robust and articulate with the distal end of radioulna. Central 2 is separated from the Distal 4 + Central 3, which is subtriangular in outline when viewed anteriorly. Distal carpals are not readily distinguishable. The prehallux is not preserved. Preserved metacarpals are very long and slender. Proximal phalanges are also elongate. Distal phalanges have not been preserved, and thus, the phalangeal formula is unknown.

Fig. 4. Skeletal reconstruction of *Cratopipa novaolindensis* nov. gen. et sp.

The pelvic girdle shows long iliac shafts, with the preacetabular

length representing nearly half the snout-vent length of the entire individual. The iliac shafts are slightly anteriorly divergent. Ilia show well-developed and fused "U"-shaped interiliac symphysis. The iliac shaft is suboval in contour, and has an anteroposteriorly extended dorsal crest. We were not able to find a well-defined dorsal tubercle on ilium. The pubis is strongly ossified.

The femur is relatively elongate and slender. It is subequal in length to the tibiofibula; its length representing nearly half of the snout-vent length. In lateral view the femur is sigmoidal in contour. The tibiofibula is long and slender. It shows slightly expanded proximal and distal ends. The tibiale and fibulare are fused to each other at their proximal and distal ends. This element is relatively short, representing two and a half times the length of the tibiofibula. Tarsal elements have not been preserved.

The metatarsals are elongate, and roughly represent more than half the length of the tibiofibula. All preserved metatarsals are subequal in length. Phalanges are very long and slender. Poor preservation precludes detailed description or the determination of the phalangeal formula. Distal claws are subtriangular in shape and distally pointed.

The body outline of *Cratopipa* nov. gen. is represented by faint impressions of pigmented skin around the skeleton. The body seems to have been slender; the hindlimbs were robust, particularly the thickened thighs.

5. Discussion

Cratopipa nov. gen. clearly belongs to Pipimorpha on the basis of the presence of several derived features, namely the presence of a large azygous frontoparietal bone, large otic capsules, fused sacrum and urostyle, and strongly expanded sacral diapophyses (Estes and Reig, 1973; Estes, 1975; Báez, 1981; Báez and Trueb, 1997; Trueb and Báez, 2006). Present analysis indicates that *Cratopipa* nov. gen. is nested within a South American clade of pipimorphs, sharing the presence of seven discrete presacral vertebrae, transverse processes of presacral IV strongly oriented anteriorly, and the iliac shaft is dorsoventrally compressed (see Aranciaga et al., 2018). In addition to the synapomorphies indicated below, *Cratopipa* nov. gen. shares with South American extinct taxa *Shelania* and *Saltenia* additional features, which include short anterior nasal process of nasal bones and the presence of a frontoparietal with posteriorly convergent margins, presence of a well-developed and acute antorbital process in the maxilla, edentulous maxillary arcade, and posteriorly expanded otic capsules that reach the posterior level of occipital condyles (Báez, 1981; Báez and Púgener, 1998). It is noteworthy to mention that the convex shape and lateral expansion of the skull roof of *Cratopipa* may be reminiscent to living species of the extant South American genus *Pipa*. However, in extant *Pipa* members, the squamosals lack an anterior expansion for contacting the maxilla, the maxillae are strongly reduced, frontoparietals are strongly transversely expanded on its anterior end, and the premaxillae are large and plate-like, which among a large number of additional anatomical details, distinguish these taxa from *Cratopipa* nov. gen. and other extinct South American pipimorphs (Báez, 1977).

Despite the high number of shared characters, the presence of vaulted margins of the frontoparietal with transverse ridges and grooves, distinguish *Cratopipa* nov. gen. from other South American forms, in which the frontoparietal lacks such thickened crests and any kind of ornamentation (e.g., *Saltenia, Shelania,* "*Xenopus*" *romeri*; Estes, 1975a,b; Báez, 1981; Báez and Trueb, 1997; Báez and Púgener, 1998). Detailed comparisons with South American extinct pipimorphs are as follows. *Cratopipa* nov. gen. differs from the Paleogene Patagonian genus *Shelania* (Casamiquela, 1961, 1065; Báez and Trueb, 1997; Báez and Púgener, 1998) in having unfused nasals, and a transversely wide frontoparietal bone with expanded flanges at its posterior end. Further,

Cratopipa nov. gen. differs from *Shelania pascuali* in having an elongate first rib (notably shortened in *Shelania*; Báez and Trueb, 1997), strongly expanded proximal end of humerus and radius-ulna, subequal-sized femur and tibiofibula (much larger femur in *Shelania*; Báez and Trueb, 1997), and proportionally short tibiale + fibulare that do not reach half the length of the tibiofibula (more than half in *Shelania*; Báez and Trueb, 1997).

Cratopipa nov. gen. resembles the Late Cretaceous *Saltenia* (Reig, 1959; Estes and Reig, 1973; Báez, 1981) in the proportionally large and subequal sized first to third ribs. However, it differs in important features, namely the anterior half of the frontoparietal bone that in *Saltenia* is transversely expanded and shows convex edges, whereas in *Cratopipa* nov. gen. it is transversely narrow and has laterally concave margins. Further, parasagittal frontoparietal crests are absent in *Saltenia* (Báez, 1981). *Cratopipa* nov. gen. has a very robust radioulna and proportionally short tibiale + fibulare that do not reach half the length of the tibiofibula (more than half in *Saltenia*; Báez, 1981). Further, *Cratopipa* nov. gen. has an anteriorly located antorbial process of the maxilla, whereas in *Saltenia* is placed approximately at the mid-length of the bone (see Báez, 1981).

The Late Cretaceous Patagonian *Kuruleufenia* differs from *Cratopipa* nov. gen. in having very narrow and smooth frontoparietal crests (Gomez, 2016), which contrast with the thick and ornamented ones present in *Cratopipa* nov. gen. Further, the latter differs from the Paleogene Brazilian "*Xenopus*" *romeri* in having thickened frontoparietal crests, in having a longitudinally concave median frontoparietal bone, and in the otic capsules being anteroposteriorly shorter and transversely wider (Estes, 1975a,b).

The Paleogene Patagonian genus *Llankibatrachus* differs from *Cratopipa* nov. gen., and resembles more derived xenopodines in the strongly expanded sacral diapophyses (Báez and Púgener, 2003). In addition, *Cratopipa* nov. gen. differs from *Llankibatrachus* in the different conformation and ornamentation of the frontoparietal bone, in the contact between the maxilla and squamosal, in the elongate first rib, and the proportionally short tibiale + fibulare that do not reach half the length of the tibiofibula (more than half in *Llankibatrachus*; Báez and Púgener, 2003). Finally, *Cratopipa* nov. gen. differs from the early late Cretaceous Patagonian *Avitabatrachus* in retaining contact between the maxilla and squamosal, robust humerus and radioulna, edentulous arcade, and first rib subequal to ribs two and third (Báez et al., 2000).

Báez et al. (2009) described a possible pipimorph from the same stratigraphic unit and a locality near the *Cratopipa* nov. gen. fossil site. The specimen consists of a disarticulated postcranium with few valuable anatomical details. However, some proportions of the available elements suggest that it could constitute a different taxon from *Cratopipa* nov. gen. The specimen described by Báez et al. (2009) shows the tibiale + fibulare that are subequal in length with the metatarsals, whereas in *Cratopipa* nov. gen. the metatarsals are markedly longer. Further, Báez et al. (2009) indicate that the lower jaw is very short, contrasting with the elongate lower jaw bones reported for *Cratopipa* nov. gen.

In summary, *Cratopipa* nov. gen. is readily distinguishable from other known fossil pipimorphs from South America and constitutes a valid and diagnosable taxon.

5.1. Phylogenetic analysis

A phylogenetic analysis was conducted with the purpose of assessing the phylogenetic relationships of *Cratopipa novaolindensis* nov. gen. et sp. with other pipimorphs (see Materials and Methods section). The analysis resulted in four most parsimonious trees (MPTs), of 583 steps in length that resulted in a single consensus tree (Fig. 5) having a Consistency Index of 0.40, and a Retention Index of 0.71. Bremer
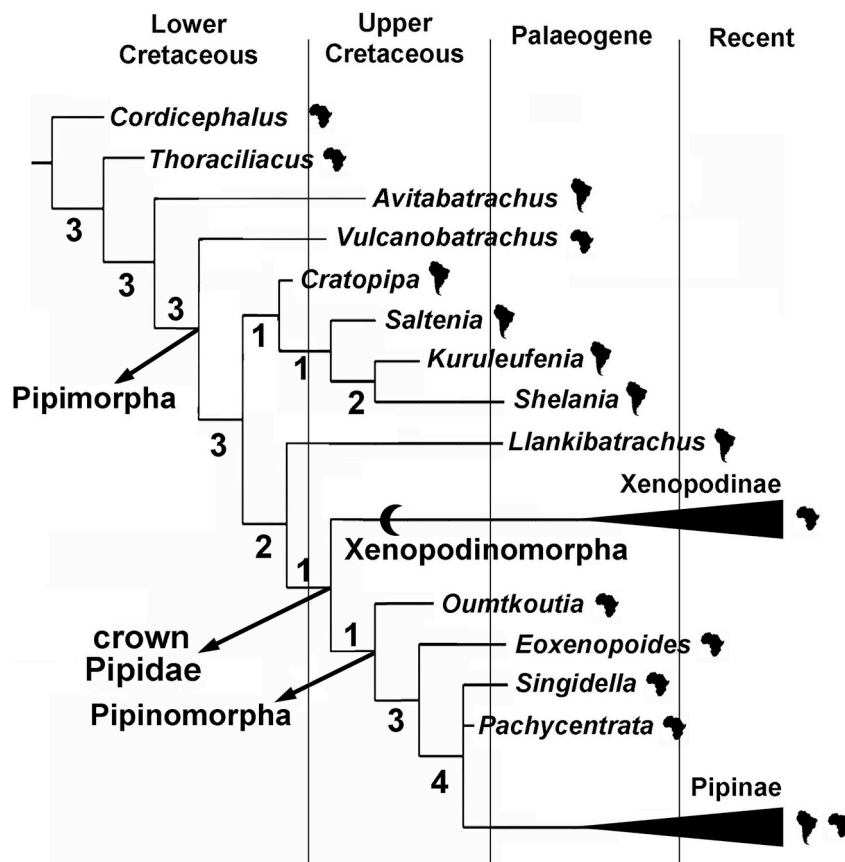
Fig. 5. Cladogram showing phylogenetic relationships, age, and geographic distribution among the more advanced Pipimorpha of *Cratopipa novaolindensis* nov. gen. et sp. Numbers indicates Bremer Support values.

Support and absolute frequencies were calculated with the aim to test the robustness of tree branches. A second round of decay was performed searching possible overflowed trees. Most nodes have low Bremer Support Values, in agreement with previous analyses made on the basis of this data matrix (e.g., Gomez, 2016; Aranciaga et al., 2018).

The topology of the tree differs in some aspects with those published by previous authors (Báez and Púgener, 2003; Báez et al., 2009; Gomez, 2016). The most impressive result is the recognition of a South American pipimorph clade composed by the genera *Cratopipa* nov. gen., *Saltenia, Shelania,* and *Kuruleufenia.* This clade is the sister group of crown pipids and is sustained on the basis of four unambiguous synapomorphies: 7 discrete presacral vertebral elements (ch. 82–1), transverse process of presacral IV markedly anteriorly oriented (ch. 94–2), dorsoventrally compressed distal iliac shaft (ch. 137–2), and ribs of the second presacral vertebra are anteriorly oriented (ch. 174–1). Most of these features were previously described and analyzed in the literature, and were often considered as derived features shared by South American pipimorphs (Báez and Trueb, 1997; Báez and Púgener, 2003; Báez et al., 2009; Gomez, 2016). The inclusion or removal of *Cratopipa* nov. gen., "*Shelania*" *laurenti* and "*Xenopus*" *romeri* in the phylogenetic analysis did not result in a strongly different topology, and the South American lineage is recovered in all trees.

On the other hand, *Llankibatrachus* is nested as the sister group of crown pipids, on the basis of the following synapomorphies: widely expanded sacral diapophyses (ch. 98–2), clavicle fused to scapula (ch. 108–2), and unexpanded ribs (ch. 175–0). Xenopodinomorpha resulted as the sister group of Pipinomorpha + *Oumtkoutia* sharing absence of preorbital process of maxilla (ch. 39–0), moderately anteriorly directed

transverse process of presacral vertebra IV (ch. 94–2), rounded posterior margin of frontoparietal bone (ch. 166–0), posterior margin of otic capsules at level with posterior margin of occipital condyles (ch. 168–0), and squared-shaped centrum of presacral vertebrae (ch. 172–0). A clade formed by Xenopodinomorpha and Pipinomorpha with exclusion of extinct South American pipimorphs is a novel result, and will be analyzed in more detail elsewhere. The clade *Oumtkoutia* + Pipinomorpha rests on the basis of a single synapomorphy: basal process of otic capsules poorly differentiated from the rest of prootic (ch. 59–0). Because this condition is ambiguous in several fossil taxa its scoring in the data matrix is problematic, and this trait may be also present in other non-pipinomorphan pipids. In consequence, the close relationship between *Oumtkoutia* and Pipinomorpha rests on weak evidence. Finally, Pipinomorpha (ch. 44–1; ch. 51–1; ch. 136–1) and Xenopodinomorpha (ch. 24–1; ch. 34–0; ch. 53–1; ch. 54–1; ch. 84–1; ch. 101–1; ch. 107–1; ch. 109–0; ch. 138–2; ch. 139–2; ch. 141–1; ch. 148–0; ch. 156–1) are recovered as monophyletic clades, in agreement with most previous phylogenetic proposals (see Báez and Trueb, 1997; Báez and Púgener, 2003; Gomez, 2016). A more detailed discussion of pipimorph phylogeny is beyond the scope of the present contribution. A more elaborate discussion is being published elsewhere (Aranciaga et al., 2018).

5.2. Palaeobiogeographical implications

The description of *Cratopipa novaolindensis* nov. gen. et sp. has a deep impact on the understanding of the early evolution and biogeography of pipimorph anurans. The present phylogenetic analysis

resulted in the inclusion of *Cratopipa* nov. gen. within an endemic South American clade of basal Pipimorpha. This is in agreement with an hypothesis envisaged by some previous authors (e.g., Báez and Púgener, 2003; Báez et al., 2008; Gomez, 2016) that argued that the several features shared between latest Cretaceous and Paleogene South American pipimorphs may be indicative that these forms constitute a monophyletic clade.

In the present phylogenetic analysis the Paleogene Patagonian genus *Llankibatrachus* lies outside such a clade, being sister to the more derived African xenopodine *Xenopus*. Further, the South American genus *Pipa* is well-nested among African fossils and *Hymenochirus* and its kin. This results in that different pipimorph lineages are present both in Africa and South America, having deep implicances in palaeobiogeography of the clade.

Matthew (1915), Noble (1922) and Darlington (1957) proposed that most anuran clades, including pipimorphs, originated in Laurasia and later dispersed to Gondwana by Late Jurassic or Early Cretaceous times (see also Feller and Hedges, 1998). However, most other authors agreed that early pipimorphs should be formerly distributed in tropical zones of Africa and South America (Casamiquela, 1961; Estes, 1975; Cannatella and De Sá, 1993; Trueb et al., 2005; 2005; Báez and Púgener, 2003; Gomez, 2016), and Reig (1958) went further in sustaining a Southern Hemisphere origin of the clade. The finding of *Cratopipa* nov. gen. reinforces the idea of an ancient presence of the clade in the continent and constitutes the oldest definitive pipimorph fossil for South America and one of the oldest records in the world (but see Estes et al., 1978, for a possible pipoid of Hauterivian-Barremian age).

Because there is general agreement that South America and Africa remained attached until Aptian times (e.g., Plestch et al., 2001), some authors suggested that pipimorphs were distributed along Gondwana in pre-Albian times and its current distribtuion may be the result of the breaking of former Gondwanan landmasses (Casamiquela, 1961; Estes, 1975; Cannatella and De Sá, 1993; Trueb et al., 2005; 2005; Báez and Púgener, 2003; Gomez, 2016). In spite that pipimorphs were present in the early Cretaceous of South America and Northern Gondwana, Israel (Nevo, 1968; present contribution), the present phylogeny indicates a more complex paleobiogeographic scenario for the clade.

In this sense, Buffetaut and Rage (1993) indicate that because anurans are intolerant to marine water, it was unlikely (although not impossible) that pipimorphs may have arrived to South America by crossing the sea. Thus, they proposed that pipimorphs were island-hopping immigrants that dispersed through an island chain or land-bridge formed by the Walvis Ridge-Rio Grande Rise passage (from now on WARISIA), during Paleocene times. This hypothesis was more recently sustained by Cannatella (2015), who suggested that pipimorphs may have migrated from South America to Africa and vice versa by the earliest Tertiary through an island chain connecting both continents. In fact, in agreement with the later hypothesis, our phylogeny shows several interleaved South American and African pipimorph clades. This contrasts with the South America-Africa vicariance distributional model, or a single westward directed floating island model (see Estes, 1975b), suggesting several bidirectional dispersal events between both landmasses.

In the same line, Bonaparte (1984 see also Rage and Vergnaud-Crazzini, 1978; Peters and Storch, 1993), sustained that faunistic similarities between early Tertiary faunas of South America and Europe may be explained by a dispersion from Africa to South America using WARISIA. This hypothesis is in agreement with minimal divergence times between several South American and African extant plant and animal groups that are calibrated well after the purported severing between both landmasses, suggesting an unlikely high number of transoceanic dispersal events between Africa and South America (see

details in Ezcurra and Agnolín, 2012). Ezcurra and Agnolin (2012; see also Oliveira et al., 2010) built upon this evidence a new palaeobiogeographical model to explain these unexpected patterns. They propose that faunistic similarities between Europe, South America and Africa may be the result of interchange through an island chain or a land-bridge (i.e. WARISIA) connecting the latter two landmasses by Late Cretaceous and early Paleogene times. Recent authors reinforced such a belated faunistic connection between Africa and South America based on distribution of extant and fossil herpetofauna, including skinks (Pereira and Schrago, 2017), amphisbaenians (Vidal et al., 2008), tortoises (Hofmeyr et al., 2016), and anurans (Agnolín, 2010). This model was also recently supported by new data coming from geographical distribution of extant and fossil plants (Katinas et al., 2013; Lin et al., 2015; Calviño et al., 2015), invertebrates (Oliveira et al., 2010; Paladini et al., 2017), fishes (Friedman et al., 2013) and birds (Angst et al., 2013; Agnolín, 2016; Selvatti et al., 2016).

In summary, our phylogeny indicates that the geographical distribution of pipimorphs by the Cretaceous and Paleogene was very complex, and several interchanges occurred through an island chain or bridge (WARISIA) connecting South America and Africa.

5.3. Palaeoenvironmental implications

The new species of Pipimorpha was found in a succession of rhythmic carbonates. The analysis of Warren et al. (2017) in the macro-, meso-, and microscopic features of the Crato Formation show the biologically induced mineralization and the existence of metabolic activity of microbes during the formation of the laminites. These authors also considered that the biomat growth may also have played a major role in the exquisite preservation of the fossils found in this lithostratigraphic unit.

The bones of *Cratopipa* nov. gen. are articulated and almost completely preserved three-dimensionally. In some cases the bones show partial crushing. They are of a brownish to yellowish color, and impressions of soft tissues surround some bones, and portions of the skin are present. Menon and Martill (2007) considered that anoxic bottom waters and high salinity might inhibit macro-scavengers, resulting in carcasses remaining intact for a long time. The Crato Formation is a hypersaline lake with anoxic botton waters, in which life was only common in freshwater tongues developed around the mouths of rivers entering the lacustrine basin. In those environments the water was less saline than in other areas, and the vegetation was abundant (Selden and Nudds, 2012). The possibility of rich food resources in these environments provided an adequate habitat for frogs (Fig. 6). The fossil anurans found in the Crato Formation (Báez et al., 2009) show that episodic freshwater influx in the lake lowered the salinity and promoted water level fluctuations (Neumann et al., 2003). Like other tetrapods, the anurans have drifted or been blown into the Crato lagoon as allochthonous elements of the biota (Selden and Nudds, 2012). In sum, pipimorphs inhabited river mouth areas and upon death, the frogs floated and drifted to another, more saline, part of the lake, where they sunk into anoxic bottom waters.

The taphonomic studies of Iniesto et al. (2017) can explain the kind of preservation of the holotype specimen of *Cratopipa novaolindensis* nov. gen. et sp. These authors conducted systematic observations of the pattern and decomposition sequence of a pipid frog with the aim of evaluating soft tissue preservation. The process of preservation shows rapid entombment in bottom sediments (25–30 days), mediated by the formation of a sarcophagus built by a complex microbial community. Then it is possible that the frog carcass maintained a variety of soft tissues for years, including cells, adipocytes, muscles and connective tissues. Later, other soft tissues could be mineralized in a Ca-rich carbonate phase (encephalic tectum) or enriched in sulphur residues

Fig. 6. Reconstruction in life of the Aptian Pipimorpha *Cratopipa novaolindensis* nov. gen. et sp. (Art by Deverson da Silva, Pepi).

(integumentary system). Mineralization processes could be more diverse than simple heterotrophic biofilms. The experiments of Iniesto et al. (2017) showed that frogs in microbial mats presented a significant delay in decay of soft tissues, and the body maintained its articulation for years. This is a reasonable interpretation for the exquisite preservation of *Cratopipa* nov. gen.

As indicated by geological evidence this lake probably showed vertical stratification of their water mass. Temperature and dissolved substances contribute to density differences in water. As demonstrated by Boeher and Schultze (2008) density differences in water bodies facilitate evolution of chemical differences with deep consequences for living organisms. As indicated by the evidence afforded by geology and paleontology *Cratopipa* nov. gen. lived nearside a meromitic lake. This kind of lacustrine ecosystem shows a chemically distinct bottom layer, that has continuously been present for at least one annual cycle. This is due to higher concentrations of dissolved substances that increased density sufficiently to resist deep recirculation and avoids exchange rates with the mixolimnion. A meromixis can also be the result of decomposition of organic material in deep water of a lake and dissolution of its final products. The organic material may be allochthonous or the primary production of photosynthetically active plankton in the epilimnion. The surface inflowing streams allowed more humid periods, dissolving the salinity of the lake's superficial environment and allowing the flourishment of freshwater animals, like the anurans. The hydrologic connection with freshwater runoff entering the lake can estabilish new patterns of water circulation (Boeher and Schultze, 2008).

6. Conclusions

Cratopipa novaolindensis nov. gen. et sp. is one of the best preserved

anurans from the Araripe Basin. This record constitutes the oldest for the Pipimorpha in South America and has a great importance for pipimorph biogeography and evolution. Present phylogenetic analysis sustains previous biogeographical hypotheses proposing a late dispersal of pipimorphs between Africa and South America through an island chain or continental bridge across the Atlantic Ocean. *Cratopipa* nov. gen. also contributes to the understanding of the ecological aspects of the depositional environment of the Crato Formation. This taxon probably lived in freshwater tongues extended around mouths of rivers that flowed into a hypersaline lacustrine basin.

Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2019.03.005.

Appendix A. Characters added to Gómez (2016) data matrix

166. Frontoparietal, shape of the posterior margin: 0, rounded; 1, convergent margins resulting in an acute posterior end of the bone.
167. Lateral flange on pterygoid: 0, absent; 1, present.

168. Posterior margin of otic capsules: 0, at same level of the occipital condyles; 1, posteriorly expanded, surpassing the posterior margin of the occipital condyles.

169. Frontoparietal, shape of the anterior margin: 0, acuminate or truncate; or 1, rounded.

170. Frontoparietal, interorbital constriction: 0, present; 1, absent.

171. Prootic, with epiotic prominences on its medial margin: 0, absent; 1, present.

172. Vertebrae, shape of centrum in dorsal view: 0, squared (almost as anteroposteriorly long as transversely wide); 1, rectangular (two or three times wider than long).

173. Sacrum, shape of diapophyseal processes: 0, anterior and posterior process rounded; 1, anterior process tapering an posterior process rounded; 2, anterior and posterior processes tapering.

174. Second pair of ribs: 0, laterally or posterolaterally projected; 1, anterolaterally oriented.

175. Transverse processes, expansions along the shaft: (0) present; (1) absent.

176. Illium, shape in dorsal view: 0, anterior half of iliac shaft subparalell each other; 1, anterior half of iliac shaft divergent each other, resulting in a V-shape contour.

Changes on character codification for *Saltenia ibanezi*, based on newly collected specimens (Aranciaga et al., 2018): Character 8, from ? to 1; Character 10, from ? to 0; Character 21, from ? to 0; Character 99, from 0 to 1; Character 109, from ? to 1; Character 112, from ? to 0; Character 113, from ? to 1; Character 114, from ? to 1; Character 149, from 1 to 2; Character 155, from ? to 1.

Appendix B. Data matrix

Data matrix. References: ?, missing data or not applicable; polymorphisms between brackets.

Alytes_obstetricans
00000000000001100010000100000001100000000000001010000000?10010010 00001101000101011011000000010101020002000100001000001010110111000000?01 010211000??0020001011110100100001001001

Ascaphus_truei
0000000000000000000[12]000000000000010000000001001?01000011000?101000 000000000000000000000100000000000000000[01]00000001001000110000?1011010000 010000?????00??0011001011010101001000001?[01]0000

Avitabatrachus_uliana
10?1?0??????????132100?010000111?0?????101?0?????0?12000?1111????0000? 011?11???00?2?0011[34]110?0??1?1????031?011000??0??????0010????????1[01]11 0000?00??1?221000?0?0?????????0?????0000

Bombina_variegata
00000000000001100010000100000001000000000000001010000000?10010000 00000001000100011011110000120102020001000100000[01]00000101001100100002 00110200?00??01200010011101002000001102111

Chelomophrynus_bayi
?0?10010??00011?10200?????????00?1?0000000??00?00?0200010???010100?0? ????0??0?010100?1?22?1???0?321????021?011200?01???????1101?1?????????1220??? 0??0200??0?1200??03????0101?01?

Cordicephalus_gracilis
1001000?00000100132000001000101?0000010?1000??0??11001?101?????000 0??1?100?0?0??2?0???[34]1?[01]101011020002100110000?00??????0?01?????100?1? 11001???0???1?1???1??100????010100110011

Discoglossus_pictus
00000000000001100010000000000001100000001000000101000000?10010000 00001101000101011001110100010100100020001000010000010101101110000101 01322100220001000101101010010000001000000

Eoxenopoides_reuningi
101100011?0110001320?010100001011?0010101?10??00?110?1?1101????000 0??11120??????3?0???3100112011102011310?10?0?00??????0???????????111100? ??00???12[01]00?1??110????001011100000

Gracilibatrachus_avallei
10?10?001?0????01?2?0000?0?0000100?0000001??0?0?0?0?????10?????????0?? ??001?????200111?1001001?10?000021?0110?01?1???????0??0????00??1??0??????1 2????2100????200?????00020110011

Hadromophryne_natalensis
00000000000001101000000000000001100000100000000101001010?0010?00 00001101000100120001121000002200100020000100110000300?1101???10002010 0??00?01200010001001010110200001000000

Hymenochirus_boettgeri
10111110101????01??111???001111011?2120101111?10101201101101000001 11?111213100113121214120012011212213110210001021000210002001?113001112 00112022112221001001111?100000002000

Neusibatrachus_wilferti
10?10000??000??000??0132?0000?0000001?000?000?0?????00?00?0???10????000?? ?1??10????01??11140?01001210?00?021?011010??0??????0?0?0????????1010??2??? 12???2100?0??100????000?11[01]0000

Oumtkoutia_anae

???1????1???????1???1??????0??????????????0???0??0??0?010110?021?0?00????
??????????0?????1?????1?????????????????????????????????????0?10000?????22
110?1?????????????????????

Pachycentrata_taqueti
???1?110011?????1??11??????101?????????????1???01?11001011010101001011
??????????????20214?3?????1?2??211310???????????????????????????????????????
???????????????????????????

Palaeobatrachus_grandipes
100101010000011013200001100001010 0?001?0010101?00?010?0?10100100000
0??1?000?0?0003?0011[34]100100121100001200011010101???????0110?0??00??1??
0??21??12??12100?1??200??0?000010110010

Pelobates_cultripes
0001011001000110010000000001000220000000010000 00100[01]100010?000100
00000000010101001100011111001202221210030000110010100120 0?110111010001
0000?????10??00200010002000003010000001010

Pipa_carvalhoi
10111010101????01321101010010110101111010101111?101002001111011?00110
11111121400011210121412010201121221?31101101010210001100300 0111301112
1000110222122200010011011?100001002111

Pipa_pipa
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11011111112400011210021412010[01]0112122113110110101021000111 0020001113
0011210001102221222000101111011?100000002111

Platyplectrum_ornatum
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0000110100010112000213010000022 2?000021100210100000 0300?110111?10101010
1322100130001000100110011 03?000000?????

Pseudhymenochirus_merlini
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Rhadinosteus_parvus
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0?????000?????????0?0???1

Rhinophrynus_dorsalis
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000000101100000100011201000003210101021101120000111??00?110111?10001010
0?????00??002000100120001030000010 00001

Saltenia_ibanezi
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2]1?0????0???2??00?1??110?????11111111110

Shelania_pascuali
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??00101?11120?0?1111?0?[12]?111[01]0?2011 11210031001100011 0???????002010??
????11210000?00???22100?1??110??01011100102111

Kuruleufenia_xenopoides

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12210??????????????????10????

Llankibatrachus_truebae
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[12]???????????2???0????110??01011100112000

Silurana_tropicalis
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Singidella_latecostata
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?0201?22?1001?1210?1??100010002000

Spea_multiplicata
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100020000??00?10??0020001000 2001?030000-1002111

Thoraciliacus_rostriceps
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Vulcanobatrachus_mandelai
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Xenopus_laevis
11110001100110001320101110100113101001010110 1?1000001[01]111121011?
00101[01]11120201111[12]11011[23]1[01]11120112121[01]03101200101 1010001100
02010110000111220 10?0211022101011011011010010111102000

Xenopus_muelleri
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11122010?0211022110110110110010000?????

Xenopus_wittei
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010111202011111111121011120112 12[01]003101200101101000110002010?10000
10121010?0201022110110110110010000?????

Cratopipa_novaolindensis
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???0??1??110?????1?101112011

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