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A review of the fossil record of caecilians Gymnophiona (Tetrapoda; Lissamphibia; Gymnophionomorpha) with comments on its use to calibrate molecular timetrees[RS1]

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Abstract:

Gymnophiona, popularly known as caecilians, the most poorly known major taxon group[RS2][MOU3] of extant amphibians, includes are elongated and limbless tetrapods, with compact ossified skulls and reduced eyes, mainly adapted to fossorial life as adults(only the Typhlonectidae exhibits adaptations for an aquatic or semiaquatic behavior). Caecilians are poorly represented in the fossil record, and despite the scarcity low number of fossil specimens described until now (only four named taxa, in addition to indeterminate fragmentary material), their fossils play a key role in the our knowledge of Lissamphibia origin and evolution, as well as contribute directly to a better understanding of phylogeny, taxonomy, and biogeography of extant gymnophionan taxa. These records are scattered throughout geological time (from the Jurassic to the sub-recent Neogene) and space (they are represented only on North and South America and Africa). Here, we revisit the caecilian fossil record, providing a brief description of all known extinct taxa described so far, along with general remarks about their impact on systematics, time range and geographic distribution of the clade, as well as prospects for future research. Possible calibration constraints based on the caecilian fossil record are provided.

Key words: Amphibians – Caecilians – Fossils – Gymnophiona – Timetree calibration - Vertebrate Paleontology

Introduction

The crown-clade Lissamphibia (see Laurin et al., 2020, for a review; but see Dubois, 2004, for an opposing view on the use of this nomen) comprises the extant taxa Anura, Urodela, and Gymnophiona. Although lissamphibians are diverse in present day biotas (Frost, 2020), their fossil record is relatively scarce, and includes only a few, but important, specimens whose preservation status is sufficiently satisfactory to allow detailed diagnoses (e. g. Schoch & Millner, 2004; Marjanović & Laurin, 2019[MOU4]). This scarcity is particularly pronounced for gymnophionanscaecilians. For many years, only one gymnophionan caecilian was known in the fossil record (Estes, 1981), and to date only four extinct taxa originally assigned to this group were have been erected named and described in details (Estes & Wake, 1972; Jenkins & Walsh, 1993; Evans & Sigogneau-Russel, 2001; Pardo et al., 2017).

The clade Gymnophiona is moderately diverse, with approximately 214 known extant species (AmphibiaWeb, 2020Frost, 2020). Popularly known as caecilians, these animals are well adapted to a fossorial existence, as shown by their elongated body, the absence of limbs and girdles, a compact and well-ossified skull, and reduced or vestigial eyes (e.g. Taylor, 1968; Duellman & Trueb, 1994; Wilkinson & Nussbaum, 2006; Wilkinson et al., 2011). However, a subgroup of gymnophionans, the typhlonectids, exhibits an aquatic or semi-aquatic lifestyles[MOU5] (Taylor, 1968; Tanner, 1971). Other distinct characteristics of caecilians include a dual mechanism for jaw closing and a pair of sensitive organs between the eyes and nostrils, known as tentacles (Wilkinson & Nussbaum, 2006).

The first now-accepted caecilian fossil species described was *Apodops pricei* Estes & Wake, 1972, a crown-gymnophionan from the Early Eocene of Brazil consisting only of an isolated pre-cloacal vertebra (see Estes & Wake, 1972 and Estes, 1981, for comments about two fossils named earlier, a silurid catfish and a cephalopod, previously misidentified as caeciliansDuellman & Trueb, 1994). Later, *Eocaecilia micropodia* Jenkins & Walsh, 1993, found in Early Lower Jurassic rocks of Arizona, the United States, was described based on numerous specimens with cranial and postcranial elements, including limbs and girdles, both completely lost in all extant species, but predictable in stem-gymnophionans (Jenkins et al., 2007). Subsequently, a taxon from the Lower Cretaceous of Morocco, *Rubricacaecilia monbaroni* Evans & Sigogneau-Russel, 2001, was erected based on a nearly complete pseudodentary, although with other isolated jaw elements, vertebrae, and a possible femur have beenalso attributed to it.

Chinlestegophis jenkinsi Pardo et al. 2017, from the Triassic of Colorado,the United States, was initially interpreted as the sister-group of caecilians. It is represented by partially preserved skulls, jaws and disarticulated postcranial elements. This enigmatic taxon may be important to understand gymnophionan evolution, because it is interpreted as showings a combination of caecilian synapomorphies and lissamphibian plesiomorphies that suggests polyphyly of extant amphibians, according to (Pardo et al. (2017). However, the affinities close relationship of *Chinlestegophis* with and gymnophionans are is controversial. Marjanović & Laurin (2019: 144 and figure 30) reanalyzed the data and showed that this is just one of four equally most parsimonious results, with the others being highly incongruent with the hypothesis of Pardo et al. (2017) *Chinlestegophis* is more likely to be a stereospondyl, but its affinities with gymnophionans are more dubious. Similarly, Carroll & Currie (1975), and more recently Anderson et al. (2008), suggested a sister-group relationship between the Early Permian lepospondyl *Rhynchonkos* and caecilians. However, a detailed CT-scan analysis of *Rhynchonkos*its morphology suggested that similarities previously regarded as synapomorphies between the recumbirostran microsaurs and gymnophionans (such as the presence of a retroarticular process, an expanded ossification in the antotic region, and a cultriform process of parasphenoid) result from ambiguities in previous character definitions and convergent evolution due to a fossorial ecomorph (Szostakiwskyj et al., 2015).

Although the fossil record of caecilians is undoubtedly scarcepoor, our present knowledge is provides sufficient clues of their past history to allow a more comprehensive approach, combining information from both extinct and extant taxa, to provides important clues to their past history. Here, we provide a review of the gymnophionan caecilian fossil record and discuss aspects of the anatomy, taxonomy, phylogeny, and biogeography of extinct groups, as well as their implications for our understanding of the biology and relationships of extant gymnophionanscaecilians.

Phylogeny and Classification of caecilians

The classification and definition of Gymnophionan caecilian clades varies according to authors. Trueb & Cloutier (1991) proposed to restrict the term names Apoda Oppel, 1811 for the crown-group of caecilians and Gymnophiona Rafinesque-Schmaltz, 1814 for the stem-total group including Apoda. However, the fact that the former name was preoccupied by several earlier nomina (Dubois, 2004), along with a possible misunderstanding in some statements about caecilian characteristics (such as the generalization of the limbless condition of gymnophionans), led some authors to reject these definitions (e.g. Dubois, 2004; Wilkinson & Nussbaum, 2006).

Furthermore, as pointed out by Wilkinson et al. (2011), the use of the name Gymnophiona for the crown-group is already well established in the literature, and a changinge in it wouldill probably bring more problems than create solutions. To avoid this problematic situation, Thus, Marjanović & Laurin (2008a) proposed the term Gymnophionomorpha for the a branchstem-based clade that comprises extant caecilians plus extinct taxa, such as *Eocaecilia. micropodia* and *Rubricacaecilia. monbaroni.*, Marjanović & Laurin (2008a) proposed the term Gymnophionomorpha.

According to the stembranch-based definition of Gymnophionomorpha, this clade comprises all lineages more closely related to the crown-clade Gymnophiona than to Batrachia. Therefore, this taxon encompasses *Eocaecilia. micropodia*, *Rubricacaecilia. monbaroni*, and extant caecilians (Figure 1). Under the phylogeny proposed by Pardo et al. (2017), it would also include *Chinlestegophis. jenkinsi*, and all other eryopiform temnospondyls (including stereospondyls and archegosaurids)stereospondyls, plus other (but not all) temnospondyls, such as archegosaurids and eryopoids. On other phylogenies, Mmembers of the Gymnophionomorpha (under their currently accepted delimitation) are characterized by numerous bone fusions, such as the lower jaw consisting in only two bones, known as pseudodentary and pseudoangular; and most of the braincase of only one, called os basale (Jenkins et al. 2007).the presence of pseudodentary and pseudoangular forming the lower jaw, os basale and absence of tympanic ear.

Recent large-scale molecular analyses strongly corroborate the monophyly of extant Lissamphibia with respect to Amniota, and most also find caecilians placed as the sister-group of Batrachia, which consists of includes Anura and Urodela (Irisarri et al., 2017; Vijayakumaret al., 2019Frost et al., 2006; Pyron & Wiens, 2011). These results also stand in a total evidence analysis (Pyron, 2011) based on a molecular data set designed to be combined with a mainly fossil-oriented data matrix (Vallin & Laurin, 2004). However, recent morphological approaches designed to test the phylogenetic affinities of lissamphibians within an expanded taxon sampleing of Paleozoic tetrapods have resulted in fundamentally distinct hypotheses on the origin of the group (most recently reviewed in see Ruta & Coates, 2007; Marjanović & Laurin, 2019). Currently there are three main phylogenetic hypotheses try to explain this question, all of which display minor variants (Figure 2). The first (Figure 2A) considers that Lissamphibia is a monophyletic group inside Temnospondyli (e.g. Trueb & Cloutier, 1991; Ruta & Coates, 2007). The second (Figure 2B) also recognizes the monophyly of lissamphibians, but nested within Lepospondyli (e.g. Marjanović & Laurin, 2008a, 2009, 2019). The third (Figures 2C and 2D) suggests that extant amphibians do not actually form a monophyletic group, because frogs and salamanders are temnospondyls and whereas caecilians are lepospondyls (e.g. Anderson et al., 2008; Huttenlocker et al., 2013) and thus more closely related to Amniota. In the variant of Anderson et al. (2008), In some variants, gymnophionans are more closely related to amniotes than to batrachians (e.g. Anderson et al., 2008), whereas this is contradicted by nearly all molecular (e.g. Irisarri et al., 2017), total evidence (Pyron, 2011), and some paleontological (Marjanović & Laurin, 2009, 2019) phylogenies.

The hypothesis recently proposed by Pardo et al. (2017) is compatible with molecular phylogenies to the extentin that the extant amphibians form a clade that excludes the amniotes (Figure 2E). According to this hypothesis, caecilians and batrachians had separate origins, with caecilians being nested among stereospondyls, whereas batrachians are dissorophoids. However, as showned by Marjanović & Laurin (2019) after a reanalyzises of these data (including the modifications suggested by Dilkes, 2015), this topology is only one of four equally most parsimonious resultsnot robust. In the other three scenarios: 1) *Chinlestegophis* is a stereospondyl, unlike caecilians; 2) neither *C. jenkinsi* nor the caecilians are stereospondyls, but both are nested within Lissamphibia; and 3) the entire Lissamphibia are stereospondyls.

In any case, tThere is no consensus about the phylogenetic relationships between the three extant groups of amphibians and their Paleozoic relatives, and more evidence from distinct data sources, such as developmental biology, CT-Scan, and molecular data, can must be used to discriminate between the various hypotheses (e.g. Szostakiwskyj et al., 2015).

Time Range of Gymnophionomorpha

Due to the scarcity limited nature of the amphibian fossil record, time divergence estimates are relatively inaccurate and vary considerably according to the methodology and data source used (Marjanović & Laurin, 2007). Some works suggest that the appearance of the amphibian crown occurred most likely in the Early Carboniferous, approximately 318–-359 Ma (e.g. Pyron, 2011; Pardo et al., 2017). However, other subsequent studies found a much younger origin for amphibians, in the Permian, approximately 300–250 Ma ago (e.g. Marjanović & Laurin, 2007; 2008b). There is no consensus on this, but any further tests should use fossil data, including stem caecilians, to achieve robust results.

If *Chinlestegophis. jenkinsi* (along with many other temnospondyls) is indeed a gymnophionomorph, then the origin of Lissamphibia and thus Gymnophionomorpha occurred during the Late Carboniferous (Pardo et al., 2017). Although these results age estimates are congruent with some previous time divergence time estimates based on molecular data (e.g. Roelants et al., 2007; Zhang & Wake, 2009; San Mauro, 2010), it isthey are incompatible with others (e.g. Marjanović & Laurin, 2007). It isAlthough

Pardo et al.’s (2007) estimates are compatible with the divergence times obtained from total- evidence tip dating of by Pyron (2011), but itthey is incompatible with its the latter’s topology. Clearly, more evidence is required to corroborate this Pardo et al. (2017) hypothesis has not been sufficiently corroborated to be considered well-supported.

The two other caecilian stem lineagestaxa, represented by *Eocaecilia. micropodia* and *Rubricacaecilia. monbaroni*, date from the Early Jurassic and the Early Cretaceous, respectively. The age of the crown-group Gymnophiona is poorly constrained, with estimates ranging from Early Lower Jurassic, approximately 188 Ma (Kamei et al., 2012) to about 100 Ma, near the Jurassic/Cretaceous boundary (Marjanović & Laurin, 2007; Pyron, 2011). Fossils attributed to the caecilian crown are limited to isolated remains, mainly vertebral elements too fragmentary to allow a more specific taxonomic assignment. They are known, in time sequence, from the Cretaceous of Sudan and Bolivia (Evans et al., 1996; Gayet et al., 2001), Paleocene of Bolivia (Rage, 1991), Eocene of Brazil (Estes & Wake, 1972) and Algeria (Gardner & Rage, 2016), Miocene of Uganda and Colombia (Hetch & LaDuke, 1997; Rage & Pickford, 2011), and Quaternary of Mexico (Wake et al., 1999).

ThereforeIn summary, the gymnophionomorph fossil record is poor, most of it associated withconsisting of stem-group taxa of Mesozoic age and fragmentary remains of Cenozoic crown-group taxa (Figure 3). This low quality in thelimited fossil record hinders limits its use for molecular clock calibrations, and limits hinders interpretations of paleobiogeographical patterns.

Gymnophionomorpha Geographic Distribution

Extant caecilians show have a pantropical distribution, occurring in South and, Central and North America, East and West Africa, Seychelles, India, Sri Lanka and Southeast Asia (Wilkinson & Nussbaum, 2006; Zhang & Wake, 2009). The entirely crown-group Cenozoic fossils were found in places within or near the geographic distribution area of modern taxa, while the most ancient remains of undoubted gymnophionomorphs come from nortsouthern [ML6]North America and northern Africa (Figure 4), regions not occupied by any extantantin which caecilians are now extinct (Pyron, 2014).

Accounting for the gymnophionomorph fossil record at the beginning of the Mesozoic, a distribution concentrated at least in northern Pangea is well established (Pyron, 2014). However, either a northern origin followed by dispersal into Gondwanaaustral lands or a southern origin and subsequent radiation to the Laurasia septentrional areas were proposed , as observed by (e.g. Feller & Hedges, 1998; Evans & Sigogneau-Russell, (2001). The gymnophionan crown-clade was probably already widespread in southern landmasses prior to its breakup during the Cretaceous, as shown by the predominantly Ggondwanan distribution of extant taxa (Duellman & Trueb, 1994), and the Cretaceous record of *Rubricacaecilia. monbaroni* (Duellman & Trueb, 1994; Evans & Sigogneau-Russell, 2001). However, the presence of *Eocaecilia* in North America is compatible raises the possibility ofwith a Laurasian origin of Gymnophionomorpha.

Therefore, bBecause of its scarcitypaucity, the gymnophionomorph fossil record provides limited biogeographical data, and informations from extant taxa, instead of fossils, are preferably usedmore helpful in evaluating biogeographic hypotheses (e.g. Gower et al., 2002; Loader et al., 2007). Mainly with the dDiscovery of new and more complete caecilian crown fossils and ancient Gondwanan stem-group remains, paleontological data cancould help to elucidate the biogeographic patterns of Ggymnophionomorphan biogeography and evolution. [ML7]

Reasons for the scarcity of Gymnophionomorpha in the fossil record[RS8]

Although the ecology and behavior of caecilians remain poorly documented (e.g., Jared et al., 1999, 2018; Measey & Herrel, 2006; Wilkinson et al., 2008; Kouete et al., 2012), when adults most they are known to be fossorial or surface cryptic, except for the highly nested typhlonectids that are aquatic or semi-aquatic typhlonectids (Ramaswami, 1941; Taylor, 1968; Tanner, 1971Ducey et al., 1993), whereas the larval stage of some speciestaxa is aquatic (e.g. Wake, 1977). The A fossorial lifestyle could, under some circumstances, facilitate fossilization by reducing significantly the negative effects associated with transport that generally occurs prior to burial (e.g. Fernandez et al., 2013). However, this would enhance fossilization only if caecilians lived in environments where sedimentation occurs, like floodplains. Given that fossorial caecilians live in the uppermost layers of emerged soil (e.g. Hebrard et al., 1992; Jared et al., 2019), they are unlikely to be fossilized there, and transport of the carcass to an environment more conducive to fossilization is unlikely, unless their body is exposed by a scavenger or by quick erosion prior to decay. Aquatic or semi-aquatic caecilians are more likely to be fossilized because some of their environments, like braided rivers and lakes, are often preserved in fossiliferous deposits (Behrensmeyer et al., 2000). Therefore, the gymnophionan fossil record is probably biased in favor of aquatic or semi-aquatic aquatic taxa who live in an aquatic or semi-aquatic environment (either as adults or larvae), and of the earliest (stem) caecilians that must probably have beenwere surface dwellers.

Other factors may contribute to the scarcity of the caecilian fossil record. One being is the fact that extant caecilians are mainly distributed in tropical regions around the world, a type of environment characterized by high levels of biological activity in decomposition and carbon cycling of remains in acid soils, hampering the fossilization process (Tappen, 1994;, but see Peterhans et al., 1993, for a different perspective). The second is related with size, because usually, larger vertebrate fossils are more noticeable than smaller ones and have a greater fossilization potential (Behrensmeyer et al., 2000), although this effect should be offset to an extent by the much greater number of small animals, which reflects obvious resource limitations (Kozlowski & Gawelczyk, 2002). Although a few caecilian species reach more than 1 m, almost the entire group is formed bymost are much smaller animals, with about a few decimeters of length (Renous & Gasc, 1989).Finally, Gymnophiona represents one of the least studied tetrapod groups, with a limited number of scientists dedicated to their study (Wilkinson & Nussbaum, 2006). Thus, the combined effects of all these factors can helpmay explain the rarity of caecilians in the fossil record.

Comparisons between extinct and extant Gymnophionomorpha

Chinlestegophis: a true gymnophionomorphan?

The skull of the Triassic *Chinlestegophis jenkinsi* has been interpreted as displaying a combination of stereospondyli plesiomorphies, along with gymnophionan and lissamphibian synapomorphies, but also exhibiting uniquely derived features (Pardo et al., 2017). Autapomorphies include a dorsomedial orbital margin formed mainly by a long anterior process of the postfrontal, a short contact between parietal and tabular, and a finger-like process of the prefrontal connected with a notch on the postfrontal.

However, plesiomorphic features typical of Ttriassic stereospondylsgocephalians also occur in concedes quite conservative traits to the skull of *Chinlestegophis. jenkinsi*. For instance, unlike extant caecilians (Wake & Hanken, 1982; Nussbaum, 1983), the lower jaw of *C. jenkinsi* is composed by almost all typical tetrapod bones, including a distinct dentary, three coronoids, a splenial, an angular, a surangular, and a prearticular (Pardo et al., 2017). Additional plesiomorphies include separated supratemporal, postparietal, tabular and occipital bones, the presence of an girdles, limbs, an otic notch, and a lateral- line sulcus (never rarely present in lissamphibians nor in most lepospondyls), even though it is restricted only to the suborbital margins of the jugal and, postorbital, girdles, and limbs. An archaic os basale, comprising only exoccipitals and opisthotics, is also interpreted as being present in *C. jenkinsi* (Pardo et al., 2017). However, fusion of exoccipital and opisthotic fusion occurs in most extant amphibians (Duellman & Trueb, 1994) and may well be an autapomorphy of Lissamphibia (Marjanović & Laurin, 2013); it is not restricted to Gymnophionomorpha.

Chinlestegophis. jenkinsi also displays possible synapomorphies with gymnophionans, including a primitive incomplete maxillopalatine (formed by the fusion of lacrimal and maxilla, but the palatine remains distinct); a double tooth row in the lower jaw; a broad cultriform process with parasagittal edges, a possible pterygoquadrate, ; and saddle-shaped occipital condyles projected relatively far beyond the posterior margin of the skull., a double tooth row in the lower jaw and a primitive, incomplete maxillopalatine (formed by the fusion of lacrimal and maxilla, but the palatine remains distinct). However, all these potential synapomorphies are problematic, as shown below.

As Pardo et al. (2017) clarifiedy in their supplements, what they interpret as a LEP (Llateral Eexposure of the Ppalatine), a structure found in several temnospondyls, could be a separate lacrimal. Indeed, the presumed LEP of *Rileymillerus cosgriffi*, an inferred close relative of *Chinlestegophis. jenkinsi*, was reinterpreted as a lacrimal by Schoch (2008: 103). The lacrimal is absent in most lissamphibians (Duellman & Trueb, 1994), although it is retained in several urodeles and albanerpetids. This bone is also absent in various stereospondyl taxa, such as brachyopoids, rhytidosteids, and *Laidleria* (Schoch, 2008). Furthermore, it is not certain that the gymnophionan maxillopalatine incorporates a lacrimal; Wake & Hanken (1982) failed did notto find one in any ontogenetic stage of *Dermophis mexicanus,* but Müuller (2006) found a small condensation above the maxilla in *Hypogeophis rostratus* and interpreted it as a lacrimal. Therefore, the status of the lacrimal (separate or fused to the maxilla) is uncertain, and the nature of the "maxillopalatine" in *Chinlestegophis* is even more dubious. The maxillopalatine certainly results from the fusion of maxilla and palatine, but both bones remain distinct in *C. jenkinsi* and *Eocaecilia. micropodia*.

Teeth of *Chinlestegophis. jenkinsi* located on the coronoids, along with the dentary row, form the typical caecilian double tooth row (Pardo et al., 2017). This character shows much homoplasy. According to Yates & Warren (2000), several other stereospondyls also have a row of coronoid teeth. These include (according to their matrix) *Dvinosaurus*, *Almasaurus*, Plagiosauridae, *Siderops*, and an undescribed genus. According to their phylogeny (Yates & Warren, 2000: fig. 1), such , a continuous coronoid tooth row appeared evolved four times in the stereospondyls that were then known: once in an unnamed clade that includes *Dvinosaurus*, *Tupilakosaurus* (in which this character was scored as unknown in the latter), and the undescribed genus, a second time in *Almasaurus*, a third time in Plagiosauridae, and a fourth time in *Siderops*. *Chinlestegophis jenkinsi* probably represents a fifth independent appearance of this character in stereospondyls, even though comparisons are hampered by differences in taxonomic sampling and topology between Yates & Warren (2000) and Pardo et al. (2017). Gymnophionans may thus represent a sixth, independent development of this character.[RS9][ML10]

AnoOther claimed shared features with caecilians comprise is a broad cultriform process with parasagittal edges, but a similar condition is seen in lysrorsophians (Wellstead, 1991; Pardo & Anderson 2016), then this character has at least some degree of homoplasy. Pardo et al. (2017) also mention a possible pterygoquadrate, but this is based partly on their inferred absence of a quadratojugal. This interpretation seems dubious because this part of the skull is not clearly shown by their scan, as illustrated by the dashed drawing of the back of the cheek in their cranial reconstruction.

Another suggested synapomorphy with gymnophionans is tThe saddle-shaped occipital condyles projecting relatively far beyond the posterior margin of the skull. This areis visible in the skull of *Chinlestegophis jenkinsi*, but it this is is present in many lepospondyls (Carroll & Gaskill, 1978), albanerpetontids (Maddin et al., 2013), and urodeles (Carroll & Holmes, 1980), so this character may diagnose a much larger clade and displays some homoplasy. Unfortunately, Pardo et al.'s (2017) matrix did not incorporate any of the scoring changes recommended by Marjanović & Laurin (2009), which resulted in important changes in the tree. IndeedWhereas, the original version of the matrix of Anderson et al. (2008), which was modified in a few intermediate versions before being incorporated into the matrix of Pardo et al. (2017), initially supported diphyly of extant amphibians, after. However, as modifications ed by Marjanović & Laurin (2009), it corroborated results retrieved a monophyletic Lissamphibia originating among lepospondyls.

If *Chinlestegophis. jenkinsi* were indeed closely related to caecilians, this would fill a major temporal gap in the fossil record of Gymnophionomorpha would be filled, but another gap would be created, underaccording to the phylogeny advocated by of Pardo et al. (2017) another major gap would be created, on the batrachian stem, between the Early Permian *Gerobatrachus* and Batrachia. However, Llissamphibians also display a large gap in their fossil record under the lepospondyl hypothesis (Marjanović & Laurin, 2008b, 2009, 2013, 2019). If *C. jenkinsi* is closely related to caecilians, features of gymnophionans interpreted as adaptations for a fossorial lifestyle, including bone fusions and loss or as well as reduction of limbs, girdles, and orbits occurred appeared more gradually than previously thought. Note however thatBut in any case, these characters show are homoplastichomoplasy and developed early in at least someother lineages because they are present in some Permo-Carboniferous lepospondyls (Carroll & Gaskill, 1978). In summary, It seems thatthere is sufficient uncertainty that the affinities of *C. jenkinsi* still representsremains an open question that will need to be evaluated in subsequent phylogenetic analyses with further revised data matrices.

Stem-Gymnophionomorpha

Several features in caecilian morphology, such as their stegokrotraphic (closed and compact skull structure, without temporal fenestrae) skull, fusion or loss of bones, and serpentiform body, were identified as adaptations for a fossorial lifestyle (e.g. Wilkinson & Nussbaum, 2006; Sherratt et al., 2014). According to phylogenies that include only extant taxa (e.g. Wilkinson, 1997), a closed skull roof evolved later in caecilian lineages, while the primitive rhinatrematids retain the plesiomorphic zygokrotraphic pattern (configuration in which temporal fenestrae are present in the posterodorsal portion of the skull). This scenario of gradual evolution towards the closure of cranial fenestrae was not corroborated with the description of *Eocaecilia.*

micropodia, which bears a well-ossified stegokrotraphic skull (Jenkins & Walsh, 1993). According to the currently accepted topology illustrated in Figure 1, the closed skull roof of extant and stem caecilians evolved independently, and therefore the primitive condition of the crown group is zygokrotraphyic (Maddin et al., 2012see Kleinteich, 2012 for a more detailed discussion on this subject).

The distinct skull morphology of caecilians skull results from numerous bone fusion and/or loss events, forming a compact cranial structure fully well adapted for a head-first burrowing style of life (Nussbaum, 1983). We can cite as examples the os basale (formed by the fusion of exoccipitals, opisthotics, prootics, parasphenoid, and basisphenoid), the maxillopalatine (comprising lacrimal, maxillae, and palatine, and possibly lacrimal), the nasopremaxillae (formed by theincluding nasals and premaxillae, but remaing as separate bones in some extant speciestaxa), the pseudodentary (formed by the coronoids and, dentary, splenial and Meckel's cartilage) and the pseudoangular (encompassing angular, articular, and prearticular) (Duellman & Trueb, 1994). Extinct taxa, despite their highly ossified skulls, also show bones that are lacking or are completely fused in extant taxa, such as jugal and quadratojugal, as expected in such ancient lineages (Jenkins et al., 2007).

The caecilian affinities of the Jurassic *Eocaecilia. micropodia* were never seriously questioned, even though Wilkinson & Nussbaum (2006) pointed out that *E. micropodia* should not be allocated in the crown-clade Gymnophiona because it lacked several of its that clade's main diagnostic characters, like especially limblessness. Indeed, sSubsequent studies confirmed that *E. micropodia* belongs to Gymnophionomorpha (e.g. Marjanović & Laurin, 2009, 2019) and that it shares a high number of braincase characteristics with gymnophionans (Maddin et al., 2012). Indeed, tThe general skull morphology of *E.*[ML11] *micropodia* closely resembles extant caecilians, including the presence of a tentacular sulcus, a completely formed os basale, and a lower jaw composed solely by a pseudoangular and pseudodentary. However, some features, like distinct palatine, jugal, quadratojugal, postparietal, and supratemporal (the last, which can alsomay be a tabular, of uncertain homology), are primitive, because in gymnophionans, these bones were lost or incorporated into in elements of compound elementsorigin (Jenkins & Walsh, 1993). Additionally, some characteristics, such as a well-developedrobust internal process in the lower jaw, are apparently unique for this taxon*Eocaecilia* (Jenkins et al., 2007).

Stem-Gymnophioniformes Marjanović and Laurin, 2008a

The fragmentaryed condition of the Cretaceous *Rubricacaecilia. monbaroni* skull clouds morphological analyses, as because only the palatine, pseudodentary, and pseudoangular are preserved. Unlike extant caecilians (Wilkinson et al., 2011), but similarly to *Eocaecilia. micropodia*, the palatine of *Rubricacaecilia. monbaroni* stays remains as a distinct bone rather than beingnot fused to the maxilla. However, differently fromcontrary to *E. micropodia*, the number of inner teeth in the pseudodentary is reduced, as in some extant gymnophionans. As in extant gymnophionans, especially rhinatrematids, the pseudoangular bears a long, straight, and well-developed retroarticular process (Evans & Sigogneau-Russell, 2001).

The number of teeth and their surface morphology (e.g. number of cusps) in gymnophionans were tentatively used for phylogenetic inferences, although some degree of intraspecific variation and numerous events of parallel acquisition likely occurred in these complexes (Wilkinson, 1991). As a rule, adult gymnophionans bear a double tooth row in the upper jaw, whereas in the lower jaw the tooth row can be either single or double, depending on the species (Wilkinson et a., 2011), and thesewith teeth are ornamented by one or two cusps (Wake & Wurst, 1979). The general tooth morphology of *Eocaecilia. micropodia* displays similarities with extant taxa, even though the teeth are more numerous and smaller than in most gymnophionans. While Whereas in *Chinlestegophis. jenkinsi* the teeth are monocuspid and apparently not pedicellate (Pardo et al., 2017), *E. micropodia* exhibits has bicuspid pedicellate teeth. Tooth morphology is poorly known in *Rubricacaecilia. monbaroni*, as because only the pedicels were preserved, but these clearly show that the teeth were pedicellate. The number of splenial inner mandibular teeth (only two per side in *R. monbaroni*) is considerably lower than in *E. micropodia*, (22 or 23 positions on each side); the systematic significance of this is difficult to assess because in the crown-group, this number varies from up to 29 in some ichthyophiids to 0zero in some ichthyophiids, dermophiids, and siphonopids and caeciliids (Evans & Sigogneau-Russell, 2001; Jenkins et al., 2007; Wilkinson et al., 2011).

Body elongation, an important gymnophionan diagnostic character (e.g. Duellman & Trueb, 1994), is also indirectly observed in ancient taxa, despite some degree of uncertainty because of the incompleteness of materials, as this trait is measured mainly by vertebrale count (Wake, 1980; Renous & Gasc, 1989). Considering extant taxa, estimates for vertebral count vary according to the authors, ranging between 70-283 (Nussbaum & Naylor, 1982) and 86-285 (Wake, 2003). A study of the evolution of the number of presacral vertabrae in lissamphibians and their presumed close relatives shows that *Eocaecilia. micropodia* shares with gymnophionans a significant increase in number of presacral vertebrae (at least 64, according to Jenkins et al., 2007); the first lissamphibian is inferred to have had about 18–-19 presacral vertebrae, whereas the last common ancestor of *E. micropodia* and gymnophionans must have had about 41 (Ascarrunz et al. 2016).

Primitive vertebrae, with a high neural spine, well-developed transverse processes, and late [ML12]neurocentral fusion (as shown by the preservation of a string of three articulated neural arches without accompanying centra), are known only for *Chinlestegophis. jenkinsi*, among potential close relatives of gymnophionans (Pardo et al., 2017). The general morphology of vertebrae in *Eocaecilia. micropodia* and *Rubricacaecilia. monbaroni* closely somewhat resembles extant groups (both present amphicoelous centra, low neural arches, medial constriction, and a ventral keel, the latter very incipient in *E. micropodia*); however, unlike extant caecilians, intercentra are retained at least in *E. micropodia*, and an interglenoid tuberculum on the atlas is present in both taxa (Evans & Sigogneau-Russell, 2001; Jenkins & Walsh, 1993; Jenkins et al., 2007).

Probably, one of the most obvious differences between stem and crown caecilians are is the presence of limbs and girdles in the former and their complete absence in the latter. Without exceptions, all extant caecilians lack both structures, but limbs were retained in most or all known stem-caecilians. In For *Chinlestegophis. jenkinsi*, preserved disarticulated appendicular elements include a clavicle, interclavicle, and a putative ulna; these are morphologically similar to those of other temnospondyls (Pardo et al., 2017). For *Eocaecilia. micropodia*, the limb size is relatively reduced, an indicative indication towards the future process that culminated in limblesnesss state condition of gymnophionans (Jenkins & Walsh, 1993). The presence of limbs is less certain in *Rubricacaecilia. monbaroni* because a femur was only tentatively attributed to it, based mainly oin the presence of trochanteric crest, a trait also observed in *E. micropodia* (Evans & Sigogneau-Russell, 2001).

Crown-Gymnophiona

With exception of the cranial material from Uganda, all crown-gymnophionan fossils are limited to isolated vertebrae. Due to their typical morphology, caecilian vertebrae are easily distinguishable, bearing in having an amphicoelous ,and medially constricted centrum, large parapophysis, low and flat neural arch, short neural spine short and a well-developed ventral keel (Wake, 1980). However, the caecilian postcranial elements, with exception of the atlas and other anteriormost vertebrae (Taylor, 1977; Wake, 1980), are not frequently used as a source of phylogenetic data, because the lack of knowledge of their variation among gymnophionan subgroups makes taxonomic assignment difficult are quite conservative among gymnophionan subgroups, according some authors (e.g. Wilkinson et al., 2011). Therefore, the attribution of such fossils to Gymnophiona seems to be unequivocal, but a more accurate and specific identifications are uncertain.

Evans et al. (1996) noted that the Sudanese fossil trunk vertebrae lack a characteristic common in Scolecomorphidae, namely the presence of a posteriorly projectinged process in the basapophyses, and thus cannot be assigned to, at least, the scolecomorphid crown. However, exclusively shared features with other African taxa are absent. The vertebra fromof Tiupampa described by Rage (1991) exhibits an amphicoelous centrum and a well-developed parapophyses; however, it is too much damaged to allow a more detailed precise identification.

In the description of the vertebra assigned to *A. pricei*, Estes & Wake (1972) noticed considered that the vertebra assigned to *Apodops pricei* its morphology and size proportions closely resemble some extant genera fromof West Africa (*Geotrypetes*) and Central America (*Dermophis* and *Gymnopis*) in morphology and proportions. Curiously, similarities with *Siphonops* and other taxa commonly found in Brazil were considered less compelling. The Colombian fossil vertebrae described by Hecht & LaDuke (1997) are morphologically similar to extant South American speciesexhibit the typical caecilian morphology, except for its size, as they arewhich is three to four times larger than the compared taxair presumed close relatives[ML13].

The caecilian material from Uganda (Rage & Pickford, 2011) represents the most complete fossil crown-gymnophionan known so far. Despite its far betterwell-[ML14]preserved condition, Rage & Pickford (2011) decided not erecting to erect a new taxon for this material. It exhibits features that are typical of caecilians, such as the pseudodentary and os basale. The Ugandan taxon retains displays [ML15]fused nasals and premaxillae and lacks a dorsal exposure of the mesethmoid. Both features are absent in the African *Herpele* and *Idiocranium*, but present in *Boulengerula*. Despite uncertainties regarding the skull roof shape, it the skull of Ugandan taxon is certainly not as zygokrotaphic as in *Scolecomorphus*. As noted by Rage & Pickford (2011), some parts of the skull are still embedded in the rock, and apparently, a new description of this material with CT-scan data is ongoing by H. Maddin (see Gardner & Rage, 2016).

Systematic Paleontology

Tetrapoda Jaekel, 1909Haworth, 1825

Amphibia De Blainville, 1816

Gymnophionomorpha, Marjanović & Laurin, 2008a

***Eocaecilia micropodia* Jenkins & Walsh, 1993**

HypodigmReferred material: represented by 40Forty specimens, stored at the Museum of Comparative Zoology, Harvard University (Massachusetts) and Museum of Northern Arizona (Jenkins & Walsh, 1993; Jenkins et al., 2007; Maddin et al., 2012).

Locality: Gold Spring, Kayenta Formation, Coconino Country, Arizona, United States.

Age: Lower Early Jurassic (Pliensbachian-Toarcian 183.7 +/- 2.7 Ma).

Main characteristics: When discovered, *Eocaecilia. micropodia* was the first stem-caecilian ever described. Of the 40 specimens assigned to this species, two preserve are almost complete skulls (Figure 6). Exclusive features of extant caecilians were observed in *E. micropodia*, as well as primitive and uniquely derived traits. Diagnostic gymnophionan characters include the presence of a sulcus anterior to the orbits (tentatively associated to with the tentacles), a complete os basale (formed by the fusion of six bones, namely the supraoccipital, exoccipital, basisphenoid, basioccipital, pleurosphenoid, and parasphenoid), and a lower jaw formed by pseudoangular and pseudodentary.

Observed primitive ancestral traits include separated unfused jugal, quadratojugal, postparital, tabular (or supratemporal), maxilla, and palatine bones (all of which are lost or fused to other bones in all extant gymnophionans) and the retention of girdles and limbs. However, as expected for a stem-gymnophionan, even the retained girdles and limbs are shortsmall, possibly indicating specialization towards the fossorial behavior. Uniquely derived characters comprise the presence of a fused stapes-quadrate, an oblique and almost planar jaw joint, a tough robust internal process of the lower jaw projected towards the adductor chamber, and a higher tooth counttotal number of teeth.

Remarks: The caecilian affinities of *E. micropodia* have never been seriously questioned and these were corroborated by various phylogenetic analyses (Maddin et al., 2012; Marjanović & Laurin, 2019), based on several braincase characters (putatively a more reliable source of morphological phylogenetic information) shared with extant taxa, such as paired dorsal and ventral olfactory nerve foramina, an elongated anterolateral processs of the sphenethmoid, and the ossifications of the nasal septum and anterior wall of sphenethmoid.

***Rubricacaecilia monbaroni* Evans & Sigogneau-Russell, 2001**

Hypodigm: The holotype comprises is a right pseudodentary **(**MCM 171), and the referred material include comprises[MOU16] two left pseudodentaries (MCM 172 and MCM 173), a fragmentaryed right pseudoangular (MCM 56), a partial palatine (MCM 174), an atlas (MCM 175), several postatlantal vertebrae (MCM 1-2; 176-181) (Evans & Sigogneau-Russell, 2001), and, possibly, a femur (MCM 3), all of them housed at the Muséeum national d'Histoire Naturelle, Paris, France.

Locality: Ksar Metlili site, Anoual, Morocco.

Age: Lower Cretaceous (Berriasian ~145-140 Ma).

Main characteristics: The skull and postcranial elements attributed to *Rubricacaecilia. monbaroni* (Figure 7), despite their fragmentary nature, reveals a morphology consistent with an ancient stem-caecilian. Among its primitive characters, there is no anterior process on the basapophyses (parasphenes), whereas such a process is found in all extant caecilians. Other primitive ancestral characters lost in extant caecilians are the possible retention of limbs (a putative femur was tentatively associated with the material) and the tuberculum interglenoideum oin the atlas.

Unlike extant caecilians, but like *Eocaecilia. micropodia* and *Chinlestegophis. jenkinsi*, *Rubricacaecilia. monbaroni* also bears a toothed palatine separated from the maxilla. The recovered pseudodentaries carry 28 narrow and deep pedicels, without preserved crowns, and exhibit numerous grooves and foramina laterally, as in extant caecilians. The pseudoangular bears internal process was small, while the caecilian typical retroarticular process, which is well developed and straight, as in rhinatrematids (not dorsally arched, as in other extant caecilians), and also has a short internal process.

Remarks: Evans & Sigogneau-Russell (2001) According the several morphologic characteristics mentioned above,interpreted *Rubricacaecilia. monbaroni* was interpreted as a stem- caecilian, but more closelyr related to the crown groups than is *Eocaecilia. micropodia.*, but considered that its The incompleteness of the specimens, along withand the tentative association of some materials justified, were used by Evans & Sigogneau-Russell (2001) to justify not carrying out a phylogenetic analysis, which could test such positioningthis hypothesis. Some recent phylogenetic analyses with morphological data have emphasized braincase characters, which are undocumented in *R. monbaroni* (e.g. Maddin, 2011; Maddin et al., 2012). Therefore, the relationship between *Rubricacaecilia* and the other gymnophionomorphans must be interpreted with caution until a cladistic analysis that includes it is carried out.

Apodops pricei **Estes & Wake, 1972**

Referred materialHolotype: the holotype (DGM 551) is limited to a single trunk vertebra (Estes & Wake, 1972), previously [MOU17]housed at Museu de Ciências da Terra, Rio de Janeiro, Brazil.

Locality: Itaboraí Basin, Rio de Janeiro, Brazil.

Age: Early Eocene (~53–-50 Ma)

Main characteristics: At the time of its discovery, *A. pricei* was the first bona fide caecilian species based on fossil material ever erected (see Estes, 1981, for comments on two other previous and now considered misidentified records). The specimen, an almost complete pre-cloacal vertebra (Figure 8), lacking only parts of prezygapophyses, parapophyses, and the posterior edge of the tip of neural arch posterior edge, and closely resemblingese extant taxa, due to shared features such as highly excavated cotyles (with chordal foramina filled by bone), general shape and proportions of centrum, neural arch, and ventral keel, as well as large and anteriorly projectinged parapophyses basapophyses.[MOU18]

Besides the well-developed ventral spine, the amphicoelous centrum also exhibits a pronounced medial constriction. Even though most of the both parapophyses have beenwere lost during the fossilization process, their broad bases can be used to infer theits large size of the processes. The neural arch is flat and low, with a short neural spine limited to its anterior half and two lateral deep groves that extends to the rib-bearing surface. The vertebra also bears two large flanges (one on each side) connecting the pre- and postzygapophyses.

Remarks: Unfortunately, the holotype (DGM 551) is currently lost (Lílian P. Bergqvist, personal communication[MOU19]). Estes & Wake (1972) recognized similarities between the vertebra of *Apodops. pricei* and some extant taxa, such as *Geotrypetes* and *Dermophis*, but they considered that features like a high degree of extensive ossification, a long and deep ventral keel, and deepest blood vessel grooves were uniquely derived, and, therefore, erected a new genus and species taxon for it. HoweverSubsequently, Taylor (1977) described some vertebrae of *Siphonops*, an extant caecilian taxon widely distributed in Brazil, and mentioned features like the well-developed ventral keel and the presence of lateral foramina that resemble those present in *A. pricei*. Accounting for the current knowledge of caecilian vertebrae, tThese structures are not unique among caecilians, and such variations can can also can be related to the positioning of the vertebra alongin the column or ontogeny (Wake, 1980), and therefore the holotype lacks diagnostic features to justify its specific status.

Furthermore, Wilkinson et al. (2011: p. 43) argued that such isolated fossilized gymnophionan vertebrae cannot confidently be attributed to families due to our incomplete knowledge of the morphological variation in extant taxa. Several collections of isolated fossil vertebrae associated with caecilians were have subsequently been described, but none werewas used to erect new species. Therefore, the designation of *A. pricei* as a valid species needs to be revaluated. However, this is out of the scope of this work and will be carried out in a further study.[MOU20]Thus, based on such considerations, we proposed that *A. pricei* be considered a *nomen dubium* until new and more complete materials are found.[RS21]

Uganda fossilTeresomata indet.

Referred material:Holotype: Nap XV 148'08, an almost complete skull with a partial lower jaw, housed at the Uganda Museum (Rage & Pickford, 2011).

Locality: Napak XV, Uganda

Age: Early Miocene (~19–-20 Ma)

Main characteristics: To date, the fossil record of crown caecilians is limited to isolated vertebrale material (see next account), with one exception: a partial skull with articulated lower jaw from the Miocene of Uganda (Figure 9). With a preserved length of 21 mm and parts missing or still embedded inside the matrix, this specimen was interpreted as belonging to a medium size caecilian (Rage & Pickford, 2011). Diagnostic caecilian features include the presence of a pseudodentary, a pseudoangular, an os basale and a typical gymnophionan skull shape (i.e. robust, semi-elliptical anteriorly, and narrower posteriorly).

In the original description, a single compressed bone, named as the dorsal table and with a surface marked by complex tubercles, was identified in the central portion of the skull roof. This arrangement, although common in other lissamnphibianurans[MOU22] (sometimes the bone is called the frontoparietal), would be unique among caecilians, as because all of them exhibit separated parietals and frontals. However, based on the published images, a suture marks can be observed partially delimiting the parietals and the frontals, as in all other gymnophionans. Notches on either side of Bordering laterally the frontals, two notches related toare the dorsalmost portions of the orbits were preservedorbital margins. The compact skull structure implies in a stegokrotraphic skull or the presence of short a narrow upper temporal fenestrae. Posteriorly, tThe specimen bears posteriorly preserves the parasphenoid portion of the os basale and two occipital condyles. Only anterior fragments of a pseudodentary (including some teeth cross sections of marginal dentitionteeth) and parts of anterodorsal and anteroventral processes of thea pseudoangular were are preserved. Between these two bones, lies a long and oblique suture.

Remarks: Specimen Nap XV 148'08 was initially attributedprovisionally referred to Caeciliidae , following the delimitation proposed by sensu Frost et al. (2006), in which Typhlonectidae and Scolecomorphidae were considered subjective synonyms of Caeciliidae to ensure monophyly of the latter. According to this taxonomy, Caeciliidae included all the gymnophionan taxa, except Rhinatrematidae and Ichthyophiidae. Wilkinson et al. (2011) proposed a different strategy to prevent Caeciliidae paraphyly, by restricting its content. Considering this scenario, Caeciliidae Frost et al., 2006 is roughly, a group equivalent to the Teresomata of Wilkinson & Nussbaum (2006). , a larger clade that comprises eight caecilian families: Caeciliidae (with a reduced content that includes only *Caecilia* and *Oscaecilia*), Herpelidae, Siphonopidae, Dermophiidae, Indotyphlidae, Chikilidae, Typhlonectidae and Scolecomorphidae (i. e. Wilkinson et al., 2011; Kamei et al., 2012). As the features of Uganda fossil caecilian, such as the presence of orbits, nasopremaxilla, posteriorly separated vomer, short or absent temporal fenestrae, also occurs in numerous teresomatan taxa, we assign Nap XV 148'08 to this clade (it can also be considered part of Caeciliidae sensu Frost et al., 2006). Given that some portions of the skull remain Furthermore, as several skull areas are embedded inside the matrix, with the use of modern techniques, as CT Scan further preparation and imaging (i.e. CT scanning), may help to reveal informativeadditional phylogenetic characters[MOU23] for making a more accurate identification phylogenetic characters can be potentially revealed and used for a more accurate assignment.

Isolated postatlantal vertebraeGymnophiona indet.

Referred material: Four trunk vertebrae (Vb-659; Vb-660; Vb-661; and Vb-781, housed at Technical University of Berlin) from Sudan (Werner, 1994; Evans et al. 1996); an isolated damaged vertebra along with (MHNC-2635, housed at the Museo de Historia Natural de Cochabamba) and other seven other vertebrae (the material is deposited in the Museo de Historia Natural de Cochabamba, but in the paper, only the collection number of a single vertebra, MHNC 8583, is mentioned,) from two localities in Bolivia (Rage, 1991; Gayet et al., 2001);, three isolated and large anterior vertebrae (IGM 183404; IGM 184791; and IGM 182186, housed at Florida Museum of Natural History) from Colombia (Hecht & LaDuke, 1997); and a single vertebra (the authors did not provide the identification number of the specimen nor the institution in which it is stored) from Mexico (Wake et al., 1999).

Localities: Wadi Milk Formation, Wadi Abu Hashim, Sudan; Santa Lucía Formation, Tiupampa, Bolivia; El Molino Formation, Pajcha Pata, Bolivia; Santa Lucía Formation, Tiupampa, Bolivia; Honda Group, La Venta, Colombia; and Paso de la Amada site, Chiapas, Mexico.

Ages: Campanian (~79.2 Ma) for Sudanese fossils; mMiddle Maastrichtian (~68.4 Ma) and Eearly Paleocene (~64–-62 Ma) for Bolivian material, Mmiddle Miocene (~13.8–-11.6 Ma) for Colombian specimens fossils, and Quaternary (1200–-1350 B.C.) for Mexican vertebrafossil.

Main characteristics: Morphologically, the caecilian postcranial axial skeleton is quite conservative. Not surprisingly, all the fossil isolated vertebrae assigned to the group exhibit the same diagnostic features, including amphicoelous centrum, broad anteroventral parapophyses, a well-developed ventral keel, and a low and flattened neural arch.

Remarks: According to Taylor (1977), anterior trunk vertebrae and, more importantly, the atlas of gymnophionans contain phylogenetic information. Unfortunately, none of these materials were preserved in a crown caecilian fossilno examples of these vertebrae are known for published fossil crown-caecilians. Therefore, due to the lack of most more specific diagnostic characters, all of the above-listed fossil vertebrae can only be these specimens were assigned to Gymnophiona indet.

Unpublished and Ppossible indeterminate records

Gardner & Rage (2016) mentioned a caecilian vertebra from the lower–middle Eocene of Glib Zegdou, Algeria. The description of this vertebra is part of a larger project on the herpetofauna from Glib Zegdou not yet published (James D. Gardner, personal communication[MOU24]). Therefore, due to the lack of information (e.g. detailed description, images, and collecting number) on this specimen, it is presented here, in a separate section from the other already published records.

An undescribed atlas (without collection number and housed at Muséum National d'Histoire Naturelle) from Colombia, was collected by Hoffstetter in 1966 and figured in Hetch & LaDuke (1997). This specimen was tentatively associated with the other vertebrae from La Venta, based mainly on their large size.

In a faunal list forof Maboko Island, Kenya, originally published by Andrews et al. (1981, table 1), a record assigned to a Miocene Nnectrideian [MOU25]was reported, but without images or detailed descriptions. Due to the significant temporal gap that this record would imply in the nectrideian fossil record (nectrideians were presumably extinct at the end of the Permian), subsequent works considered that this material is actually a lissamphibian, probably either a salamander (Van Dijk, 1995) or a caecilian (Gardner & Rage, 2016). However, until the material is reevaluated, such assignments remain uncertain, though both hypotheses are much more likely than the initial nectrideian assignment.

Possible calibration points constraints [MOU26]for Gymnophionomorpha

Calibration constraints based on the caecilian fossil record are uncommon,. Pprobably due to its scarcity, usuallybecause few fossil occurrences are available. Instead, other taxa are used, such as batrachians (e.g. San Mauro et al., 2014). Following the recommendations of Parham et al. (2012), here we provide calibrations for four three nodes of the gymnophionomorphans. We attempted to use the most recent or widely accepted age estimates for each location. Calibrations are highly dependent of on phylogeny and stratigraphy, and thus the latest, best-supported dating and phylogenetic hypotheses were considered.

GYMNOPHIONOMORPHA Marjanovic & Laurin, 2008[RS27]

Node Calibration: Divergence between the total clade of caecilians and its nearest crown sister taxon (Batrachia).

Oldest fossil: *Triadobatrachus massinoti* (Piveteau, 1936), from the Sakamena Group, Madagascar (the holotype, MHNH MAE 126, comprises an almost complete individual, and is housed at Muséum National d'Histoire Naturelle)*Eocaecilia micropodia* Jenkins & Walsh, 1993

Phylogenetic Justification: If lissamphibians and batrachians are in facare botht a monophyletic group, then the divergence time betweenage of Batrachia and Gymnopionomorpha is the same. In this scenario, the oldest fossil available is the stem-batrachian *Triadobatrachus*, from the Early Triassic of Madagascar**.** However, considering the polyphyletic hypothesis for the origin of lissamphibians, only members of the Gymnophionomorpha lineage can be used for providing constraints. In this case, the oldest fossil available is *Eocaecilia micropodia*, from the Early Jurassic of USA.[MOU28] Phylogenetic analyzes have repeatedly confirmed the relationship between *E. micropodia* and extant caecilians (e.g. Maddin et al., 2012), and its position as a sister group of all other gymnophionomorphs is supported by many characters (discussed in more detail above) and is widely accepted.

Minimum age: 181 Ma251.2 Ma (assuming lissamphibian monophyly)

Soft Maximum age: 186.4 Ma251.9 Ma[MOU29]

Age Justification: The siltstones and sandstones deposits of Kayenta Formation were historically thought to be Triassic-Jurassic or Early Jurassic age (see Lucas et al., 2005) in age. Due to the lack of available ash beds and useful stratigraphic fossils, the age estimates of such deposits were not very accurate. However, recently, the first radiometric date for the unit estimated an Early Jurassic age of 183.7 +/- 2.7, changing the temporal range of Kayenta Formation from Sinemurian-Pliensbachian to Pliensbachian-Toarcian (Marsh et al. 2015). Traditionally, estimates for the age of the Sakamena Group in Madagascar range from the Late Permian to the Middle Triassic.

Due to the absence of radiometric and magnetostratigraphic dating, age estimates are not so accurate (Benton et al., 2015). Based on palynological evidence, an Induan age was proposed for this unit (Wescott & Diggens, 1998; Nowak et al., 2018). Considering the polyphyletic hypothesis, then the oldest Gymnophionomorpha fossil available is *Eocaecilia micropodia*, from the Kayenta Formation, recently dated by Marsh et al. (2015) in 183.7 +/- 2.7 Ma (Pliensbachian-Toarcian).[MOU30]

Comment: If the hypothesis proposed by Pardo et al., (2017) were correct, the minimum age for the group would be extended to the Norian (208-227 Ma). However, we consider that calibration of the stem-node Gymnophionomorpha with *C. jenkinsi* to estimate the divergence time of gymnophionans should be avoided until its phylogenetic affinities is thoroughly tested and clarified. Until that happens, *Eocaecilia macropodia* seems to represent a better fit for this calibration constraint (Marjanović & Laurin, 2009, 2019). A large gap (approximately 67 Ma), between the origin of Lissamphibia and the first record of Gymnophionomorpha, still persists[MOU31]. It is a strong indicative on the existence of a hidden diversity, which *Chinlestegophis jenkinsi* could fill, at least partially.

GYMNOPHIONA Rafinesque-Schmaltz, 1814

Node Calibration: Divergence between Rhinatrematidae Nussbaum, 1977 and *Rhinatrema bivittatum* and Stegokrotaphia Canatella and Hillis, 1993. *Caecilia tentaculata*

Oldest fossil: Gymnophiona indet., based on four trunk vertebrae from the Late Cretaceous (Campanian) of Sudan (Werner, 1994; Evans et al., 1996).

Phylogenetic Justification: The Sudanese vertebrae exhibit a morphology typically associated with the Gymnophiona crown, including features like an amphicoelous centra, flat neural spine, prominent ventral keel and, mainly, a parapophyses strongly projected anteroventraly. Such characteristics allow safely assign the specimens to this taxon.

Minimum age: 76.82.1 Ma

Soft Maximum age: 81.6 Ma

Age Justification: Wadi Milk Formation, located in the nNorthern Sudan, includes deposits of braided river systems, interspersed laterally with sediments associated todeposited in flood plains, lakes, and meandering rivers., Hhistorically, it was considered to be Albian-Santonian in age, on the basis of palynological evidence data estimates (Schank, 1990). However, recent U-Pb radiometric dating found a much younger age for such unitof: 79.2 ± 2.4 Ma, or equivalent to theassigning it to middle Campanian (Agyemang et al., 2019).

Comment: Previously, Benton et al. (2015) proposed a Paleogene minimum age for this cladeGymnophiona, based on the record of *Apodops. pricei*. Nevertheless, t The Sudanese vertebrae share with crown-gymnophionans the presence of well-developed parapophyses, which are absent in both *Eocaecilia* and *Rubricacaecilia,* and this supports the extension ofpushing the temporal range of crown-Gymnophiona back to the middle Campanian. However, this remains tentative, because these taxa the Sudanese taxon alternatively could also fit just outside the gymnophionan crown.

TERESOMATA Wilkinson & Nussbaum, 2006

Node Calibration: Divergence between Scolecomorphidae Taylor, 1969 and a nameless group formed by Caeciliidae, Typhlonectidae, Herpelidae, Chikilidae, Dermophiidae, Indotyphlidae, and Siphonopidae.*Scolecomorphus kirkii* and *Caecilia tentaculata*.

Oldest fossil: Napak gymnophionan Nap XV 148’08, an almost complete skull articulated with a partial lower jaw from the Miocene (Burdigalian) of Uganda (Rage and Pickford, 2011).

Phylogenetic Justification: Rage and Pickford (2011) assigned this fossil to the Caeciliidae based on the combination of the following characters: posterior part of vomers clearly separated, presence of orbits, fusion of premaxillae and nasals. However, these features are present in several families of crown-caecilians (Wilkinson et al., 2011), rejecting the original allocation until a more detailed study of the material is concluded. Thus, the fossil skull from Uganda is here assigned to Teresomata based on the present understanding of caecilian systematics. As studies with the material are underway (Gardner & Rage, 2016), it has the potential to be assigned again to a less inclusive taxon within Terosomata. As Nap XV 148’08 has not yet been included in phylogenetic analyzes, its positioning is still uncertain, as it could lie outside the Teresomata crown. Therefore, this specimen can only be used to constrain the split between Ichthyophiidae and Teresomata.

Minimum age: 19 Ma

Soft Maximum age: 20 Ma[MOU32]

Age Justification: Napak XV, located in northeastern Uganda, comprises multiple fossiliferous deposits intercalated with tuffs, located on and around an ancient volcano. Dates on these tuffs, calculated with potassium-argon dating (Bishop et al., 1969), vary between 19.5 ± 2 Ma and 18.3 ± 0.4; however, the latter date is considered an anomalous result, and currently these deposits are assigned to the early Burdigalian, with an estimated age between 19–-20 Ma (Werdelin, 2010, fig. 3.4).

Comment: There is currently insufficient evidence to refer Oolder unnamed fossil caecilians from the Eearly Paleocene (Rage, 1991) and MaastrichtianLate Cretaceous (Gayet et al., 2001) of Bolivia, and Early CretaceousCampanian of Sudan (Evans et al., 1996) can potentially be associated to Teresomata. However, the evidence supporting this attribution is insufficient. Therefore, the oldest fossil that can be undoubtedly assigned to this clade is the skull Nap XV 148'08.

Conclusions

Gymnophionans remain are the most poorly known group of tetrapods, particularly in aspects of their evolutionary history. Despite the paucity of its fossil record, fossil caecilians directly affect our understanding of taxonomy, phylogeny and biogeography of extant caecilians, and they help to discriminate between hypotheses about the origin of Lissamphibia.

The gymnophionan fossil record shows wide temporal gaps, even in the Cenozoic, in which (not considering *Apodops. pricei*) no diagnostic material has been assigned to an extant species, genus, or even family so far. Therefore, the discovery of new, more complete and diagnostic fossils assignableed to the caecilian crown-group may would likely make a substantial contribution to contribute to resolvinge phylogenetic and biogeographic questions about caecilian clades and better constraining molecular clocks.

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Figure Caption

Fig. 1: Time-calibrated phylogeny of Gymnophionomorpha, considering only paleontological data, including stem lineages plus the crown-group Gymnophiona, compiled from based on the topologies of Wilkinson et al. (2011) and Evans & Sigogneau-Russell (2001). Red stippled doted lines indicates K-Pg boundary.

Fig. 2: The dDifferent proposals for the phylogenetic relationships of Lissamphibia, based on Marjanović & Laurin (2008a), Laurin et al. (2019) and Pardo et al. (2017). A) temnospondyl hypothesis. B) Lepospondyl hypothesis. C) One of the examples of polyphyly hypothesis. D) Alternative topology also related toversion of the polyphyly hypothesis. E) Topology recovered presented [MOU36]by Pardo et al. (2017). Silhouettes have been downloaded from phylopic.org. All images are under creative Commons Attribution 3.0 Unported. *Eocaecilia* and *Triadobatrachus* by Nobu Tamura; *Diplocaulus* by Gareth Monger; *Metoposaurus*, *Archaeovenator* and *Edops* by Dmitry Bogdanov.

Fig. 3: The Summary of the fossil record of Gymnophionomorpha through geological time. Solid bBlack circles indicate crown-group taxa, while whereas white ones circles with a black outline and white filling indicate stem-lineages.

Fig. 4: Geographic Ddistribution of extant caecilians, along with the locations where fossils attributed to the group were foundand fossil occurrences. Orange marks circles indicate stem- lineages, while whereas white ones circles correspond to fossils assigned toindicate crown- group taxa. 1) *Eocaecilia* (Jenkins & Walsh, 1993). 2) *Rubricacaecilia* (Evans & Sigogneau-Russel, 2001). 3) *Apodops* (Estes & Wake, 1972). 4) Isolated vertebra (Rage, 1991). 5) Seven vertebrae (Gayet et al., 2001). 6) Three vertebrae (Hecht & LaDuke, 1997). 7) One vertebra (Wake et al., 1999). 8) An incomplete skull (Rage & Pickford, 2011). 9) Four vertebrae (Evans et al., 1996). Modified from Cogger & Zweifel (1998). 1) Forty specimens assigned to *Eocaecilia micropodia*, from United States of America (Jenkins & Walsh, 1993). 2) Incomplete skull and postcranial elements assigned to *Rubricacaecilia monbaroni*, from Morocco (Evans & Sigogneau-Russell, 2001). 3) Four vertebrae assigned to Gymnophiona indet., from Sudan (Evans et al., 1996). 4) Seven vertebrae assigned to Gymnophiona indet., from Bolivia (Gayet et al., 2001). 5) Isolated vertebra of Gymnophiona indet., from Bolivia (Rage, 1991). 6) Single vertebra assigned to *Apodops pricei*, from Brazil (Estes & Wake, 1972). 7) An incomplete skull assigned to Teresomata indet., from Uganda (Rage & Pickford, 2011). 8) Three vertebrae assigned to Gymnophiona indet., from Colombia (Hecht & LaDuke, 1997). 9) One vertebra assigned to *Dermophis mexicanus*[MOU37], an extant caecilian species of Mexico (Wake et al., 1999). Modified from Cogger & Zweifel (1998) and Loader et al. (2007).

Fig. 5: Reconstructions of the *Chinlestegophis. jenkinsi* skulls in dorsal (A) and left lateral (B) views. Redrawn from Pardo et al. (2017). Abbreviations (for Figures 5, 6, 7, and 9): a, angular; ch, choana; d, dentary; dt, dorsal table; dta, dorsal tubercle of atlas; eo, exoccipital; f, frontal; fh, femoral head; imt, inner mandibular teeth; j, jugal; lep, lateral exposure of palatine; m, maxilla; mp, maxillopalatine; n, nasal; ns, nasal septum; ob, os basale; oc, occipital condyle; p, parietal; pa, pseudoangular; paf, parasphenoid; pd, pseudodentary; pf, post-frontal; pm, premaxilla; po, postorbital; pob, parasphenoid portion of os basale ; pp, post-parietal; pq, pterygoquadrate; prf, prefrontal; qj, quadratojugal; rep, retroarticular process; rpp, rostral process of parasphenoid; sa, surangular; sn, spinal nerve exit foramen; sp, splenial; sph, sphenethmoid; spm, septomaxilla; sq, squamosal; st-q, stapes-quadrate; st, supratemporal; t, tabular; tig, tuberculum interglenoideum; to, tooth. Scale bar = 5 mm.

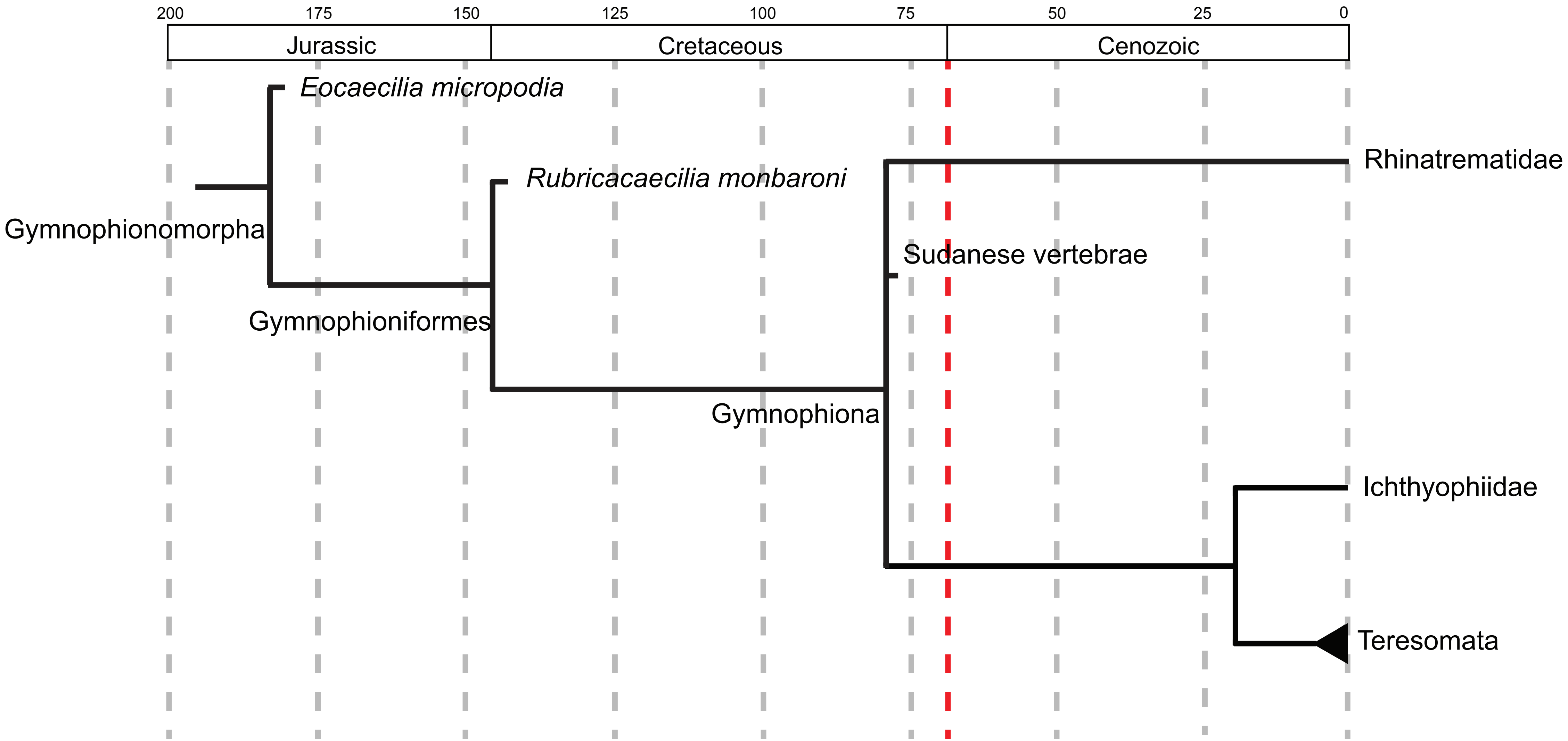
Fig. 6: Reconstruction of *Eocaecilia. micropodia* skull in dorsal (A) and right lateral (B) views. Redrawn from Jenkins et al. (2007). See Ffigure 5 for abbreviations. Scale bar = 1 mm.

Fig. 7: Reconstructions Drawnings of *Rubcricacaecilia. monbaroni* holotype (MCM 171), a right pseudodentary (MCM 171) in lingual view (A), the proximal head of a left femur (MCM 3) (B) tentatively associated referred towith the species (B), (MCM 3) and MCM 175, an referred atlas (MCM 175) in right lateral view (C). Redrawn from Evans & Sigogneau-Russell (2001). See Figure 5 for abbreviations. Scale bar = 1 mm.

Fig. 8: Holotype precloacal vertebra (DGM 551) of *Apodops pricei* in left Llateral (A), ventral (B) and dorsal (C) views of DGM 551, a precloacal vertebra assigned to *A.*

pricei. Missing parts were markedindicated with a stippleddotted lines. Redrawn from Estes & Wake (1972). Scale bar = 1 mm.

Fig. 9: Teresomata indet. incomplete skull and right lower jaw (Nap XV 148’08), in Ddorsal (A) and ventral (B) views of Nap XV 148’08, a Teresomata indet. Areas covered by rock are indicated in grey. Redrawn from Rage & Pickford (2011) and Gardner & Rage (2016). See Ffigure 5 for abbreviations. Scale bar = 1 cm.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Jurassic
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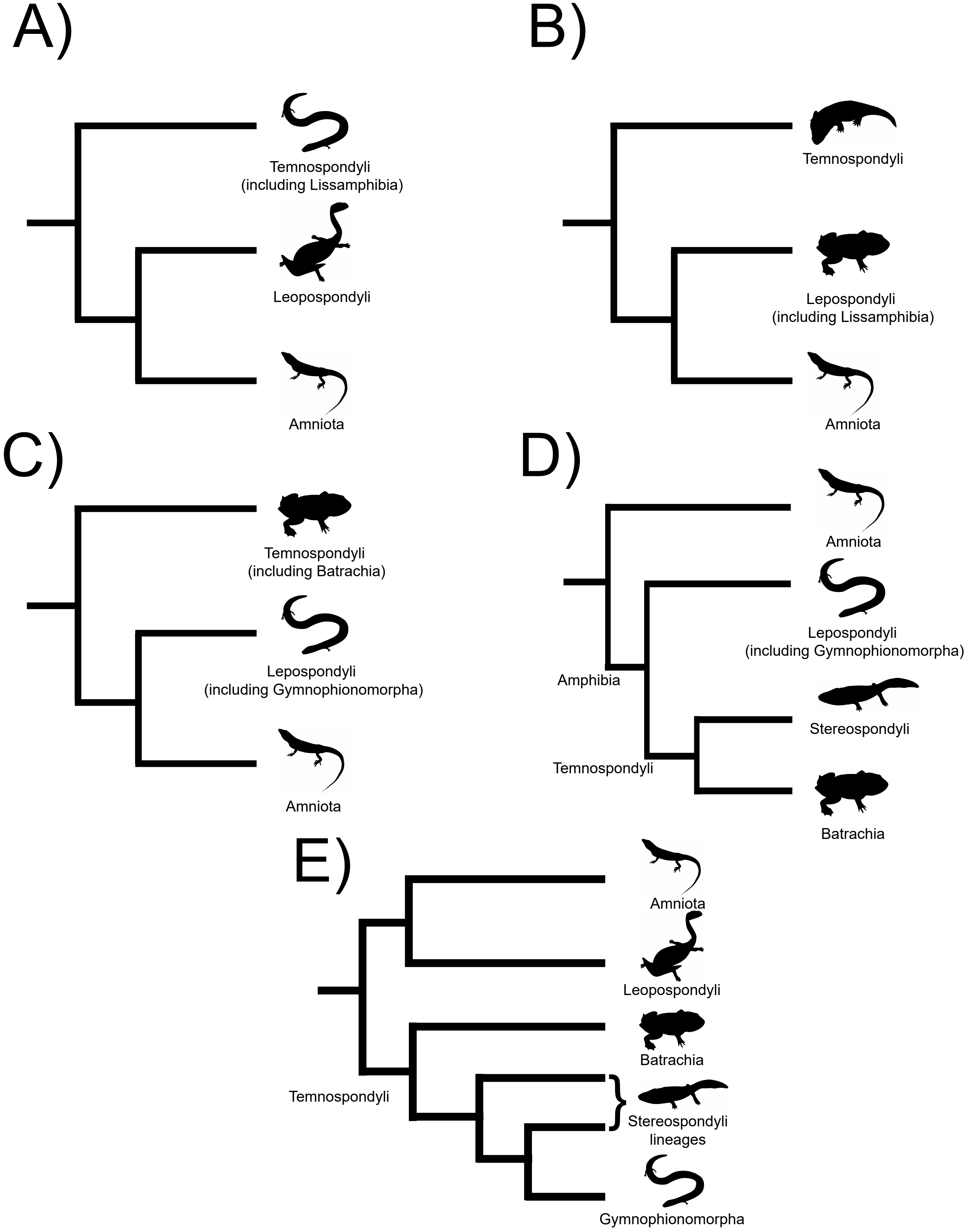
Rubricacaecilia monbaroni
Rhinatrematidae
Gymnophionomorpha
Sudanese vertebrae
Gymnophioniformes
Gymnophiona
Ichthyophiidae
Teresomata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(including Batrachia)
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Amniota
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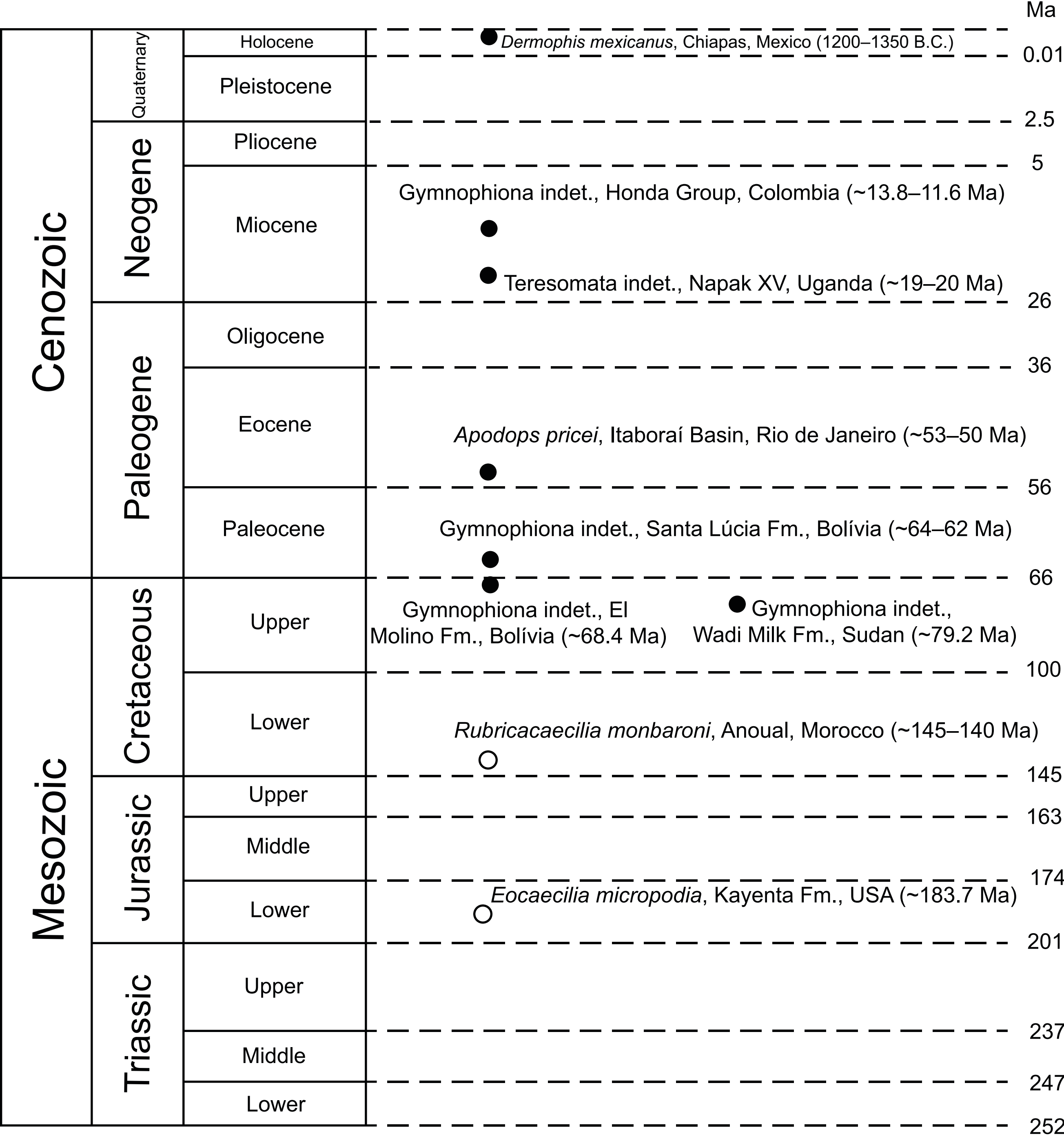
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Dermophis mexicanus, Chiapas, Mexico (1200–1350 B.C.)
Gymnophiona indet., Honda Group, Colombia (~13.8–11.6 Ma)
Teresomata indet., Napak XV, Uganda (~19–20 Ma)
Apodops pricei, Itaboraí Basin, Rio de Janeiro (~53–50 Ma)
Gymnophiona indet., Santa Lúcia Fm., Bolívia (~64–62 Ma)
Gymnophiona indet., El Molino Fm., Bolívia (~68.4 Ma)
Gymnophiona indet., Wadi Milk Fm., Sudan (~79.2 Ma)
Rubricacaecilia monbaroni, Anoual, Morocco (~145–140 Ma)
Eocaecilia micropodia, Kayenta Fm., USA (~183.7 Ma)


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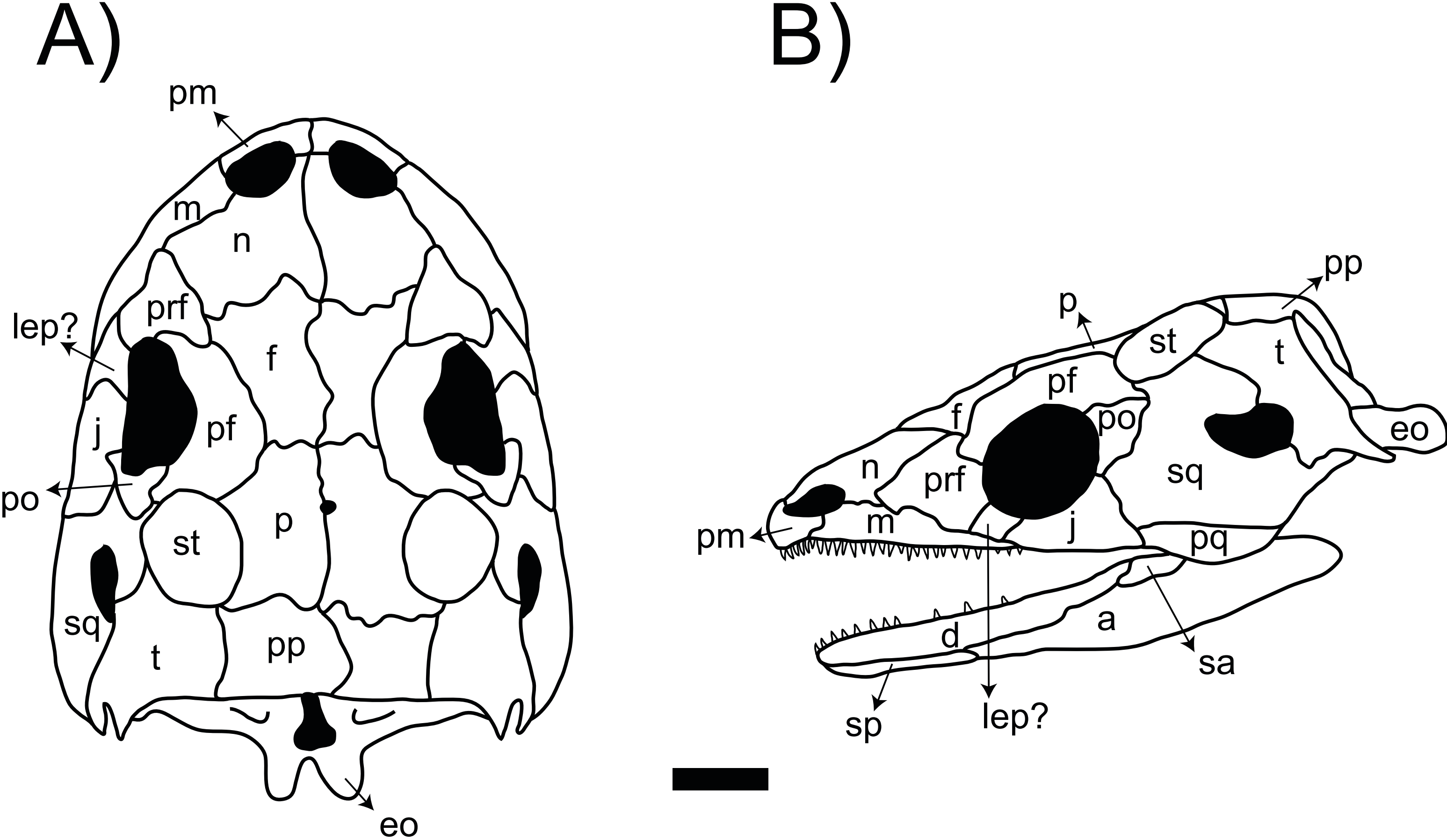
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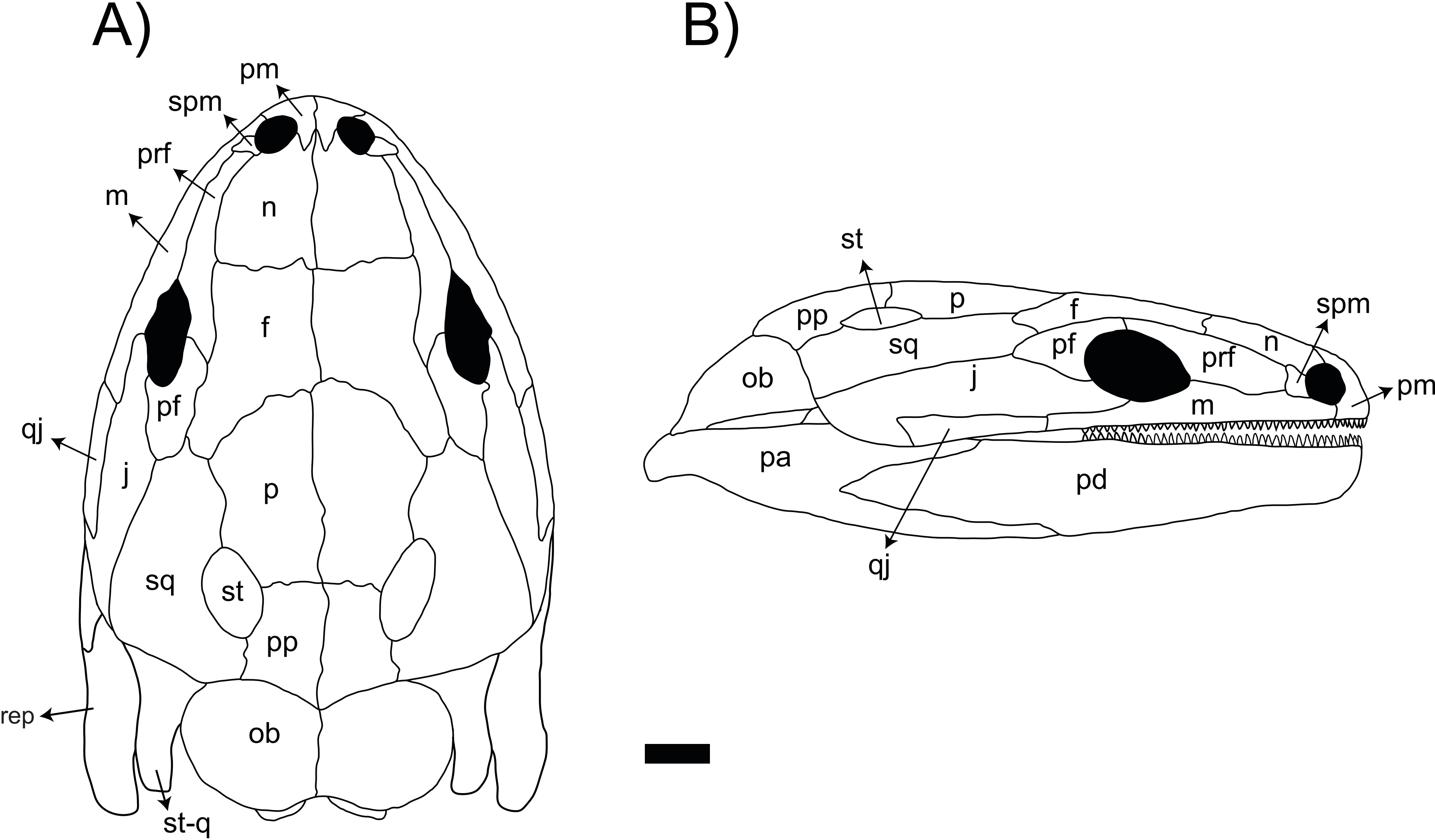
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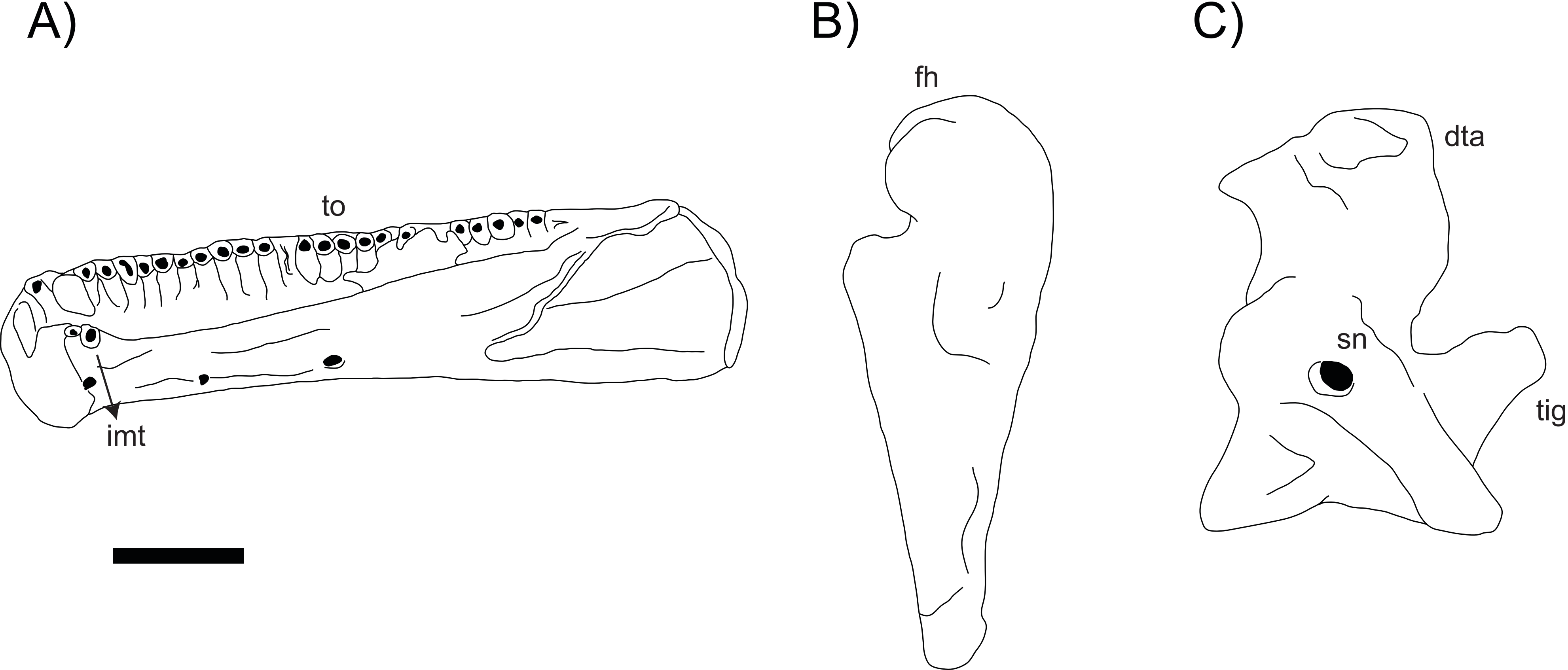
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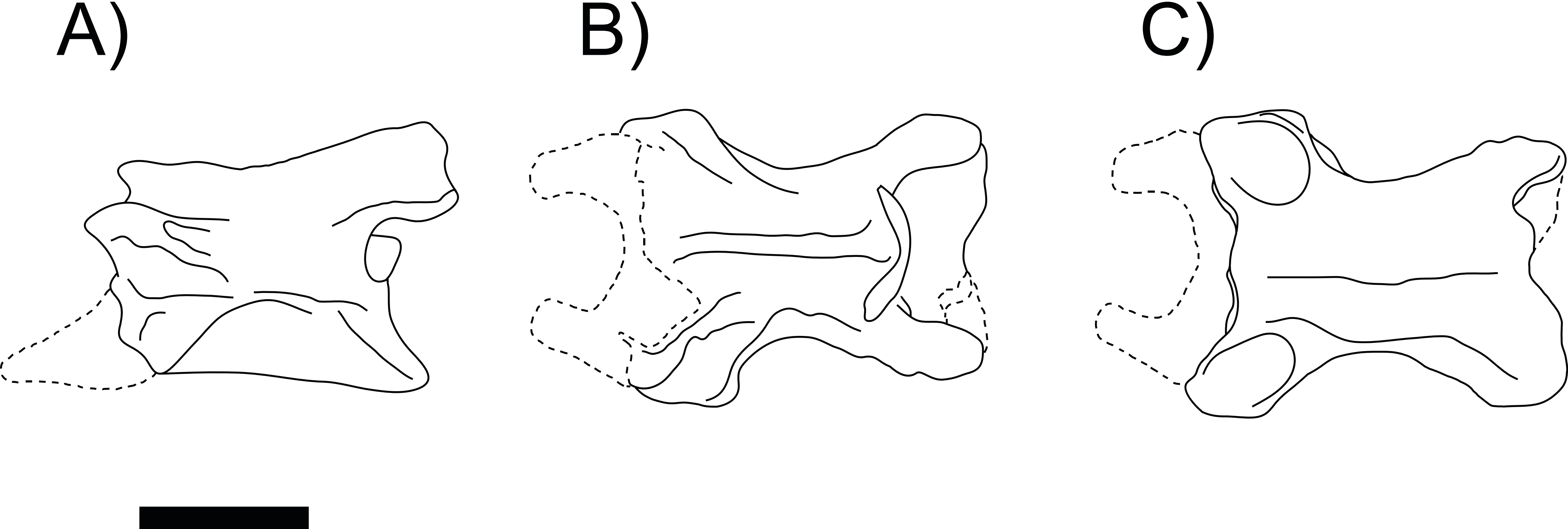
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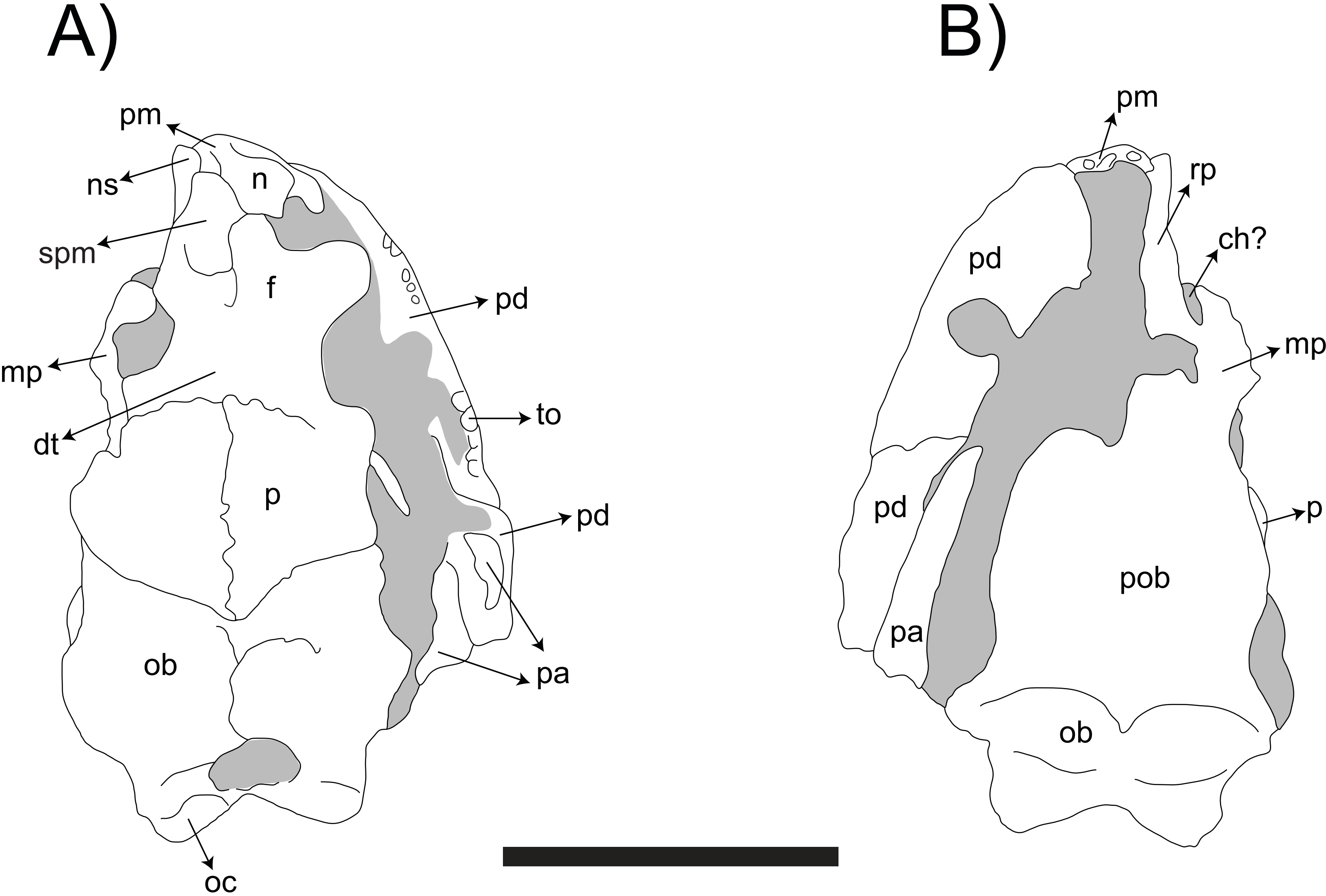
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