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

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Abstract:

Gymnophiona, the most poorly known group of extant amphibians, includes elongated limbless tetrapods, with compact ossified skulls and reduced eyes, mainly adapted to fossorial life (only the Typhlonectidae exhibits adaptations for an aquatic or semiaquatic behavior). Caecilians are poorly represented in the fossil record, and despite the low number of fossil specimens described until now (only four taxa, in addition to indeterminate fragmentary material), their fossils play a key role in the 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 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 (Schoch & Millner, 2004; Marjanović & Laurin, 2019). This scarcity is particularly pronounced for gymnophionans. For many years, only one gymnophionan was known in the fossil record (Estes, 1981), and to date only four extinct taxa originally assigned to this group were erected 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 (Frost, 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 (Duellman & Trueb, 1994; Wilkinson & Nussbaum, 2006; Wilkinson et al., 2011). However, a subgroup of gymnophionans, the typhlonectids, exhibits an aquatic or semi-aquatic lifestyle (Taylor, 1968). 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 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 (Duellman & Trueb, 1994). Later, *Eocaecilia micropodia* Jenkins & Walsh, 1993, found in Early Jurassic rocks of 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 other isolated jaw element, vertebrae and a possible femur have been attributed to it.

Chinlestegophis jenkinsi Pardo et al. 2017, from the Triassic of 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 shows a combination of caecilian synapomorphies and lissamphibian plesiomorphies that suggests polyphyly of extant amphibians, according to Pardo et al. (2017). However, the affinities of *Chinlestegophis* with gymnophionans are controversial. Marjanović & Laurin (2019: 144 and figure 30) reanalyzed the data and showed that *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 its morphology suggested that similarities previously regarded as synapomorphies between the recumbirostran microsaurs and gymnophionans 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 scarce, our present knowledge provides sufficient clues of their past history to allow a more comprehensive approach combining information from both extinct and extant taxa. Here, we provide a review of the gymnophionan fossil record and discuss aspects of the anatomy, taxonomy, phylogeny and biogeography of extinct groups, as well as their implications for our understanding of extant gymnophionans.

Phylogeny and Classification of caecilians

The classification and definition of Gymnophionan clades varies according to authors. Trueb & Cloutier (1991) proposed to restrict the term Apoda Oppel, 1811 for the crown-group of caecilians and Gymnophiona Rafinesque-Schmaltz, 1814 for the stem-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 change in it will probably bring more problems than create solutions. To avoid this problematic situation, for the stem-based clade that comprises extant caecilians plus extinct taxa, such as *E. micropodia* and *R. monbaroni*, Marjanović & Laurin (2008a) proposed the term Gymnophionomorpha.

According to the stem-based definition of Gymnophionomorpha, this clade comprises all lineages more closely related to the crown-clade Gymnophiona than to Batrachia. Therefore, this taxon encompasses *E. micropodia*, *R. monbaroni* and extant caecilians (Figure 1). Under the phylogeny proposed by Pardo et al. (2017), it would also include *C. jenkinsi*, and all other stereospondyls, plus other (but not all) temnospondyls, such as archegosaurids and eryopoids. Members of the Gymnophionomorpha (under their currently accepted delimitation) are characterized by 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 includes Anura and Urodela (Frost 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 sampling of Paleozoic tetrapods resulted in fundamentally distinct hypotheses on the origin of the group (see Ruta & Coates, 2007; Marjanović & Laurin, 2019). Currently three main 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 recognize the monophyly of lissamphibians, but nested within Lepospondyli (e.g. Marjanović & Laurin, 2008a, 2019). The third (Figures 2C and 2D) suggest that extant amphibians do not actually form a monophyletic group, because frogs and salamanders are temnospondyls and caecilians lepospondyls (e.g. 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 extent that extant amphibians form a clade that excludes 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 showed by Marjanović & Laurin (2019) after a reanalyzes of the data, this topology is not robust. In any case, there 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 be used to discriminate between the various hypotheses (e.g. Szostakiwskyj et al., 2015).

Time Range of Gymnophionomorpha

Due to the scarcity 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, 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 *C. jenkinsi* (along with many other temnospondyls) is indeed a gymnophionomorph, the origin of Lissamphibia and Gymnophionomorpha occurred during the Late Carboniferous (Pardo et al., 2017). Although these results are congruent with some previous time divergence estimates based on molecular data (e.g. Roelants et al., 2007; Zhang & Wake, 2009; San Mauro, 2010), it is incompatible with others (e.g. Marjanović & Laurin, 2007). It is compatible with the divergence times obtained from total evidence tip dating of Pyron (2011), but it is incompatible with its topology. Clearly, more evidence is required to corroborate this hypothesis.

The two other caecilian stem lineages, represented by *E. micropodia* and *R. monbaroni*, date from Early Jurassic and Early Cretaceous, respectively. The age of the crown-group Gymnophiona is poorly constrained, with estimates ranging from Early 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 caecilian crown are limited to isolated remains, mainly vertebral elements too fragmentary to allow a more specific taxonomic assignment. They are known 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), Miocene of Uganda and Colombia (Hetch & LaDuke, 1997; Rage & Pickford, 2011) and Quaternary of Mexico (Wake et al., 1999).

Therefore, the gymnophionomorph fossil record is poor, most of it associated with stem-group taxa of Mesozoic age and fragmentary remains of Cenozoic crown-group taxa (Figure 3). This low quality in the fossil record hinders molecular clock calibration and limits interpretations of paleobiogeographical patterns.

Gymnophionomorpha Geographic Distribution

Extant caecilians show a pantropical distribution, occurring in South, 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 North America and northern Africa (Figure 4), regions in 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 austral lands or a southern origin and subsequent radiation to the septentrional areas were proposed, as observed by Evans & Sigogneau-Russel (2001). The gymnophionan crown-clade was probably already widespread in southern landmasses prior to its breakup during the Cretaceous, as shown by the predominantly gondwanan distribution of extant taxa and the Cretaceous record of *R. monbaroni* (Duellman & Trueb, 1994; Evans & Sigogneau-Russell, 2001). However, the presence of *Eocaecilia* in North America is compatible with a Laurasian origin of Gymnophionomorpha.

Therefore, because of its scarcity, the fossil record provides limited biogeographical data, and information from extant taxa, instead of fossils, are preferably used in biogeographic hypotheses (Gower et al., 2002). Mainly with the discovery of new and more complete caecilian crown fossils and ancient Gondwanan stem-group remains, paleontological data can help to elucidate the biogeographic patterns of Gymnophionomorpha evolution.

Reasons for the scarcity of Gymnophionomorpha in the fossil record

Although the ecology and behavior of caecilians remain poorly documented (e.g., Jared et al., 1999, 2018; Wilkinson et al., 2008), most are known to be fossorial, except for typhlonectids that are aquatic or semi-aquatic (Taylor, 1968; Ducey et al., 1993). The fossorial lifestyle could, under some circumstances facilitate fossilization by reducing significantly the negative effects associated with transport that generally occurs prior to burial. However, this would enhance fossilization only if caecilians lived in environments where sedimentation occurs. Given that fossorial caecilians live in the uppermost layers of emerged soil, 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 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 taxa and of the earliest (stem) caecilians that must have been surface dwellers.

Other factors may contribute to the scarcity of the caecilian fossil record. One being 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, 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 by smaller animals, with 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 help 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. 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 triassic stegocephalians also concedes quite conservative traits to the skull of *C. 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 distinct dentary, coronoid, splenial, angular, surangular and prearticular (Pardo et al., 2017). Additional plesiomorphies include separated supratemporal, postparietal, tabular and occipital bones, the presence of an otic notch and a lateral line sulcus (never present in lissamphibians nor in most lepospondyls), even though it is restricted only to the suborbital margins of the jugal, 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 occurs in most extant amphibians (Duellman & Trueb, 1994) and may well be an autapomorphy of Lissamphibia (Marjanović & Laurin, 2013); it is not restricted to Gymnophiomorpha.

C. jenkinsi also displays possible synapomorphies with gymnophionans, including a broad cultriform process with parasagittal edges, a possible pterygoquadrate, 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) clarify in their supplements, what they interpret as a LEP (Lateral Exposure of the Palatine), a structure found in several temnospondyls, could be a separate lacrimal. Indeed, the presumed LEP of *Rileymillerus cosgriffi*, a close relative of *C. 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. This bone is also absent in various stereospondyl taxa, such as brachyopoids, rhytidosteids, and *Laidleria* (Schoch, 2008). Furthermore, it is not certain that the maxillopalatine incorporates a lacrimal; Wake & Hanken (1982) failed to find one in any ontogenetic stage of *Dermophis mexicanus*, but Muller (2006) found a small condensation above the maxilla in *Hypogeophis* 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 *E. micropodia*.

Teeth of *C. jenkinsi* located on the coronoid, 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 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), 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.

Other claimed shared features with caecilians comprise a broad cultriform process with parasagittal edges, but a similar condition is seen in lyrosophians (Wellstead, 1991). 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 the saddle-shaped occipital condyles projecting relatively far beyond the posterior margin of the skull. This is visible in the skull, but it 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. Indeed, 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. However, as modified by Marjanović & Laurin (2009), results retrieved a monophyletic origin among lepospondyls.

If *C. jenkinsi* were indeed closely related to caecilians, a major temporal gap in Gymnophionomorpha would be filled, but another gap would be created, under the phylogeny advocated by Pardo et al. (2017) on the batrachian stem, between the Early Permian *Gerobatrachus* and Batrachia. However, lissamphibians 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 interpreted as adaptations for a fossorial lifestyle, including bone fusions and loss or reduction of limbs, girdles and orbits occurred more gradually than previously thought. But in any case, these characters show homoplasy and developed early because they are present in some Permo-Carboniferous lepospondyls (Carroll & Gaskill, 1978).

It seems that the affinities of *C. jenkinsi* still represents 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 the stegokrotraphic skull, fusion or loss of bones, and serpentiform body, were identified as adaptations for a fossorial lifestyle (Wilkinson & Nussbaum, 2006; Sherratt et al., 2014). According to phylogenies that include only extant taxa, a closed skull roof evolved later in caecilian lineages, while the primitive rhinatrematids retain the plesiomorphic zygokrotraphic pattern. This scenario of gradual evolution towards the closure of cranial fenestrae was not corroborated with the description of *E. micropodia*, which bears a well-ossified stegokrotraphic skull (Jenkins & Walsh, 1993). According to the 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 zygokrotraphic (Maddin et al., 2012).

The distinct caecilian skull results from numerous bone fusion and/or loss events, forming a compact cranial structure fully adapted for a 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), the nasopremaxillae including nasals and premaxillae), the pseudodentary (formed by the coronoids, 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, as expected in such ancient lineages (Jenkins et al., 2007).

The caecilian affinities of the Jurassic *E. 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 main diagnostic characters, like limblessness. Indeed, subsequent studies confirm that *E. micropodia* belongs to Gymnophionomorpha (Marjanović & Laurin, 2009, 2019) and that it shares a high number of braincase characteristics with gymnophionans (Maddin et al., 2012). Indeed, the general skull morphology *E. micropodia* closely resembles extant caecilians, including the presence of a tentacular sulcus, a completely formed os basale and a lower jaw composed by pseudoangular and pseudodentary. However, some features like distinct palatine, jugal, quadratojugal, postparietal and supratemporal (of uncertain homology) are primitive, because in gymnophionans, these bones were lost or incorporated in elements of compound origin (Jenkins & Walsh, 1993). Additionally, some characteristics, such as a well-developed internal process in the lower jaw, are apparently unique for this taxon (Jenkins et al., 2007).

Stem-Gymnophioniformes

The fragmented condition of the Cretaceous *R. monbaroni* skull clouds morphological analyses, as only the palatine, pseudodentary, and pseudoangular are preserved. Unlike extant caecilians (Wilkinson et al., 2011), but similarly to *E. micropodia*, the palatine of *R. monbaroni* stays as a distinct bone rather than being fused to maxilla. However, differently from *E. micropodia*, the number of teeth in the pseudodentary is reduced, as in 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 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, gymnophionans bear double tooth row with teeth ornamented by one or two cusps (Wake & Wurst, 1979). The general tooth morphology of *E. micropodia* displays similarities with extant taxa, even though the teeth are more numerous and smaller than gymnophionans. While in *C. jenkinsi* the teeth are monocuspid and apparently not pedicellate (Pardo et al., 2017), *E. micropodia* exhibits bicuspid teeth. Tooth morphology is poorly known in *R. monbaroni*, as only the pedicels were preserved, but these clearly show that the teeth were pedicellate. The number of splenial teeth (only two) is considerably lower than *E. micropodia*, (22 or 23 positions); 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 0 in some ichthyophiids and caeciliids (Evans & Sigogneau-Russell, 2001; Jenkins et al., 2007).

Body elongation, an important gymnophionan diagnostic character (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 vertebrae count (Wake, 1980; Renous & Gasc, 1989). A study of the evolution of the number of presacral vertabrae in lissamphibians and their presumed close relatives shows that *E. micropodia* shares with gymnophionans a significant increase in number of vertebrae; 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 neurocentral fusion (as shown by the preservation of a string of three articulated neural arches without accompanying centra), are known only for *C. jenkinsi*, among potential close relatives of gymnophionans (Pardo et al., 2017). The general morphology of vertebrae in *E. micropodia* and *R. monbaroni* closely resembles extant groups; however, unlike extant caecilians, intercentra are retained 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 the presence of limbs and girdles. Without exceptions, all extant caecilians lack both structures, but limbs were retained in most or all known stem-caecilians. In *C. 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 *E. micropodia*, the limb size is relatively reduced, an indicative towards the future limbless state of gymnophionans (Jenkins & Walsh, 1993). The presence of limbs is less certain in *R. monbaroni* because a femur was only tentatively attributed to it, based mainly in 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 an amphicoelous, medially constricted centrum, large parapophysis, low and flat neural arch, 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), 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, the presence of a posteriorly projected 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 of Tiupampa described by Rage (1991) exhibits an amphicoelous centrum and a well-developed parapophyses, however is too much damaged to allow a more detailed identification.

In the description of the vertebra assigned to *A. pricei*, Estes & Wake (1972) noticed that its morphology and size proportions closely resemble extant genera of West Africa (*Geotrypetes*) and Central America (*Dermophis* and *Gymnopis*). 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 species, except for its size, as they are three to four times larger than the compared taxa.

The caecilian material from Uganda (Rage & Pickford, 2011) represents the most complete fossil crown-gymnophionan known so far. Despite its far better-preserved condition, Rage & Pickford (2011) decided not erecting 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 fused nasals and maxillae and lack 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 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 (Gardner & Rage, 2016).

Systematic Paleontology

Tetrapoda Haworth, 1825

Amphibia De Blainville, 1816

Gymnophionomorpha, Marjanović & Laurin, 2008

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

Referred material: represented by 40 specimens, stored at Museum of Comparative Zoology (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 Jurassic (Pliensbachian-Toarcian 183.7 +/- 2.7 Ma).

Main characteristics: When discovered, *E. micropodia* was the first stem caecilian ever described. Of the 40 specimens assigned to this species, two preserve 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 (associated to the tentacles), a complete os basale (formed by the fusion of six bones) and a lower jaw formed by pseudoangular and pseudodentary.

Observed primitive traits include separated jugal, quadratojugal, postparital, tabular (or supratemporal), maxilla and palatine bones (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 short, indicating specialization towards the fossorial behavior. Uniquely derived characters comprise the presence of a stapes-quadrate, oblique and almost planar jaw joint, a tough internal process of lower jaw projected towards adductor chamber and a higher tooth count.

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 (a more reliable source of morphological phylogenetic information) shared with extant taxa, such as paired olfactory nerve foramina, an elongated anterolateral processs of sphenethmoid and the ossifications of nasal septum and anterior wall of sphenethmoid.

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

Hypodigm: The holotype comprises a right pseudodentary **(**MCM 171), and the referred material include two left pseudodentaries (MCM 172 and MCM 173), a fragmented 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).

Locality: Ksar Metlili site, Anoual, Morocco.

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

Main characteristics: The skull and postcranial elements attributed to *R. 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 basapophyses, whereas such a process is found in all extant caecilians. Other primitive characters lost in extant caecilians are the possible retention of limbs (a putative femur was tentatively associated with the material) and the tuberculum interglenoideum in atlas.

Unlike extant caecilians, but like *E. micropodia* and *C. jenkinsi*, *R. monbaroni* also bears a toothed palatine separated from 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 internal process was small, while the caecilian typical retroarticular process is well developed and straight, as in rhinatrematids (not dorsally arched, as in other extant caecilians).

Remarks: According the several morphologic characteristics mentioned above, *R. monbaroni* was interpreted as a stem caecilian, but closer related to crown groups than *E. micropodia.* The incompleteness of the specimens, along with the tentative association of some materials, were used by Evans & Sigogneau-Russell (2001) to justify not carrying out a phylogenetic analysis, which could test such positioning. 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).

Apodops pricei Estes & Wake, 1972

Referred material: the holotype (DGM 551) is limited to a single trunk vertebra (Estes & Wake, 1972).

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 caecilian species based on fossil material ever erected. The specimen, an almost complete pre-cloacal vertebra (Figure 8), lacking only parts of prezygapophyses, parapophyses and the tip of neural arch posterior edge, closely resemble extant taxa, due to shared features 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 projected parapophyses.

Besides the well-developed ventral spine, the amphicoelous centrum also exhibits a pronounced medial constriction. Even though most of the parapophyses have been lost during fossilization process, the broad base can be used to infer its large size. 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 connecting pre and postzygapophyses.

Remarks: Unfortunately, the holotype (DGM 551) is currently lost. Estes & Wake (1972) recognized similarities between the vertebra of *A. pricei* and some extant taxa, such as *Geotrypetes* and *Dermophis*, but they considered that features like a high degree of ossification, long and deep ventral keel and deepest blood vessel grooves were uniquely derived, and therefore erected a new taxon for it. However, Taylor (1977) described some vertebrae of *Siphonops*, a taxon widely distributed in Brazil, and mentioned features like the well-developed ventral keel and the presence of lateral foramina. Accounting for the current knowledge of caecilian vertebrae, these structures are not unique among caecilians, and such variations can also be related to the positioning of the vertebra in the column or ontogeny (Wake, 1980), and therefore the holotype lacks diagnostic features to justify its specific status. Furthermore, Wilkinson et al. (2011:43) argued that such isolated fossilized gymnophionan vertebrae cannot confidently be attributed to families. Several isolated fossil vertebrae associated with caecilians were subsequently described, but none were used to erect new species. Thus, based on such considerations, we proposed that *A. pricei* be considered a *nomen dubium* until new and more complete materials are found.

Uganda fossil

Referred material: Nap XV 148’08, an almost complete skull with a partial lower jaw, housed at 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 vertebrae material, with one exception: a partial skull from the Miocene of Uganda (Figure 9). With 21 mm and parts missing or still embedded inside the matrix, this specimen was interpreted as a medium size caecilian. Diagnostic caecilian features include the presence of pseudodentary, pseudoangular, os basale and a typical gymnophionan skull shape (robust, semi-elliptical anteriorly and narrower posteriorly).

In the original description, a single compressed bone, named as 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 lissanphibians (sometimes the bone is called frontoparietal), would be unique among caecilians, as all of them exhibit separated parietals and frontals. However, suture marks can be observed partially delimiting the parietals and the frontal, as in all other gymnophionans. Bordering laterally the frontals, two notches related to dorsalmost portions of the orbits were preserved. The compact skull structure implies in a stegokrotraphic skull or short fenestrae. The specimen bears posteriorly the parasphenoid portion of the os basale and two occipital condyles. Only anterior fragments of a pseudodentary (including some teeth cross sections of marginal dentition) and parts of anterodorsal and anteroventral processes of a pseudoangular were preserved. Between these two bones, lies a long and oblique suture.

Remarks: Specimen Nap XV 148’08 was initially attributed to Caeciliidae, following the delimitation proposed by 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 equivalent to Teresomata 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). Furthermore, as several skull areas are embedded inside the matrix, with the use of modern techniques, as CT Scan, phylogenetic characters can be potentially revealed and used for a more accurate assignment.

Isolated postatlantal vertebrae

Referred material: Four trunk vertebrae from Sudan (Werner, 1994; Evans et al. 1996); an isolated damaged vertebra along with other seven vertebrae from Bolivia (Rage, 1991; Gayet et al., 2001), three isolated and large anterior vertebrae from Colombia (Hecht & LaDuke, 1997) and a single vertebra 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; Honda Group, La Venta, Colombia; Paso de la Amada site, Chiapas, Mexico.

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

Main characteristics: Morphologically, the caecilian postcranial 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 fossil. Therefore, due to the lack of most specific diagnostic characters, all these specimens were assigned to Gymnophiona indet.

Possible indeterminate record

In a faunal list of Maboko Island, originally published by Andrews et al. (1981, table 1), a record assigned to a Miocene Nectridia was reported, but without images or detailed descriptions. Due to the significant temporal gap that this record would imply in the nectridian fossil record (nectridians were presumably extinct at the end of the Permian), subsequent works considered that this material is actually a lissamphibian, probably 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 nectridian assignment.

Possible calibration points for Gymnophionomorpha

Calibration constraints based on the caecilian fossil record are uncommon. Probably due to its scarcity, usually 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 nodes of the gymnophionomorphans. Calibrations are highly dependent of phylogeny and stratigraphy, and thus the latest, best-supported dating and phylogenetic hypotheses were considered.

GYMNOPHIONOMORPHA Marjanovic & Laurin, 2008

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

Oldest fossil: *Eocaecilia micropodia* Jenkins & Walsh, 1993

Phylogenetic Justification: 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 Ma

Soft Maximum age: 186.4 Ma

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).

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).

GYMNOPHIONA Rafinesque-Schmaltz, 1814

Node Calibration: Divergence between *Rhinatrema bivittatum* and *Caecilia tentaculata*

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

Phylogenetic Justification: The Sudanese vertebrae exhibit a morphology typically associated with Gymnophiona crown, including features like an amphicoelus 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 Northern Sudan, includes deposits of braided river systems, interspersed laterally with sediments associated to flood plains, lakes and meandering rivers, historically considered to be Albian-Santonian in age, on the basis of palynological data estimates (Schank, 1990). However, U-Pb radiometric dating found a much younger age for such unit: 79.2 ± 2.4 Ma, assigning it to middle Campanian (Agyemang et al., 2019).

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

TERESOMATA Wilkinson & Nussbaum, 2006

Node Calibration: Divergence between *Scolecomorphus kirkii* and *Caecilia tentaculata.*

Oldest fossil: Napak gymnophionan (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.

Minimum age: 19 Ma

Soft Maximum age: 20 Ma

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 early Burdigalian, with an estimated age between 19-20 Ma (Werdelin, 2010, fig. 3.4).

Comment: Older unnamed fossil caecilians from Early Paleocene (Rage, 1991) and Late Cretaceous (Gayet et al., 2001) of Bolivia and Early Cretaceous 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 Nap XV 148’08.

Conclusion

Gymnophionans remain 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 *A. 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 assigned to the caecilian crown-group may contribute to resolve phylogenetic and biogeographic questions about caecilian clades and better constrain molecular clocks.

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References

Anderson JS, Reisz RR, Scott D, Fröbisch NB, Sumida SS. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* **453**, 515-518.

Andrews P, Meyer GE, Pilbeam DR, Couvering JAV, Couvering JAHV. 1981. The Miocene Fossil Beds of Maboko Island, Kenya: Geology, Age, Taphonomy and Palaeontology. *Journal of Human Evolution* **10:** 35-48.

Agyemang PCO, Roberts EM, Bussert R, Evans D, Muller J. 2019. U-Pb detrital zircon constraints on the depositional age and provenance of the dinosaur-bearing

Upper Cretaceous Wadi Milk formation of Sudan. *Cretaceous Research* **97:** 52-72.

Ascarrunz E, Rage JC, Legreneur P, Laurin M. 2016. *Triadobatrachus massinoti*, the earliest known lissamphibian (Vertebrata: Tetrapoda) re-examined by µCT-Scan, and the evolution of trunk length in batrachians. *Contributions to Zoology* **85:** 201–234.

Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000. Taphonomy and Paleobiology. *Paleobiology* **26:** 103-147.

Benton MJ, Donoghue PCJ, Asher RJ, Friedman M, Near TJ, Vinther J. 2015. *Palaeontol Electron* **18:** 1-116.

Bishop WW, Miller JA, Fitch FJ. 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *American Journal of Science* **267:** 669-699.

Carroll RL, Currie PJ. 1975. Microsaurs as possible apodan ancestors. *Zool J Linn Soc* **57:** 229-247.

Carroll RL, Gaskill P. 1978. *The order Microsauria.* Philadelphia: American Philosophical Society.

Carroll RL, Holmes R. 1980. The skull and jaw musculature as guides to the ancestry of salamanders. *Zool J Linn Soc* **68:** 1–40.

Cogger HG, Zweifel RG. 1998. *Encyclopedia of reptiles & amphibians*. Cambridge: Academic Press.

Ducey PK, Formanowicz DR, Boyet L, Mailloux J, Nussbaum RA. 1993. Experimental Examination of Burrowing Behavior in Caecilians (Amphibia: Gymnophiona): Effects of Soil Compaction on Burrowing Ability of Four Species. *Herpetologica* **49:** 450-457.

Dubois A. 2004. The higher nomenclature of recent amphibians. *Alytes* **22:** p. 1-14.

Duellman WE, Trueb L. 1994. Biology of Amphibians. Baltimore: The Johns Hopkins University Press.

Estes R. 1981. Encyclopedia of Herpetology Part 2, Gymnophiona, Caudata. Stuttgart: Gustav Fischer Verlag.

Estes R, Wake MH. 1972. The first fossil record of caecilian amphibians. *Nature* **239:** 228–231.

Evans SE, Milner AR, Werner C. 1996. Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan. *Palaeontology* **39:** 77–95.

Evans SE, Sigogneau-Russell D. 2001. A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. *Paleontology* **44:** 259–273.

Frost DR, Taran G, Faivovich J, Bain RH, Haas A, Haddad CFB, De Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC. 2020. The amphibian tree of life. *Bulletin of American Museum of Natural History* **297:** 1-370.

Frost DR. 2020. Amphibian Species of the World: an Online Reference. Version 6.1 (*June 6 2020*). Electronic Database accessible at https://amphibiansoftheworld.amnh.org/index.php. American Museum of Natural History, New York, 2020. doi.org/10.5531/db.vz.0001

Gardner JD, Rage JC. 2016. The fossil record of lissamphibians from Africa, Madagascar, and the Arabian Plate. *Palaeobiodiversity and Palaeoenvironments* **96:** 169-220.

Gayet M, Marshall LG, Sempere T, Meunier FJ, Cappetta H, Rage JC. 2001. Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. *Palaeogeography Palaeoclimatology Palaeoecology* **169:** 39-68.

Gower DJ, Kupfer A, Oommen OV, Himstedt W, Nussbaum RA, Loader SP, Presswell B, Muller H, Krishna SB, Boistel R, Wilkinson M. 2002. A molecular phylogeny of ichthyophiid caecilians (Amphibia: Gymnophiona: Ichthyophiidae): out of India or out of South East Asia? *Proceedings of Royal Society of London* **269:** 1563-1569.

Haddoumi H, Allain R, Meslouh S, Metais G, Monbaron M, Pons D, Rage JC, Vullo R, Zouhi S, Gheerbran E. 2016. Guelb el Ahmar (Bathonian, Anoual Syncline, eastern Morocco): First continental flora and fauna including mammals from the Middle Jurassic of Africa. *Gondwana Research* **29:** 290-319.

Hecht MK, Laduke TC. 1997. Limbless Tetrapods. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ, eds. *Vertebrate paleontology in the Neotropics The Miocene fauna of La Venta, Colombia.* Washington: Smithsonian Institution Press, 95-99.

Irisarri I, Baurain D, Brinkmann H, Delsuc F, Sire JY, Kupfer A, Petersen J, Jarek M, Meyer A, Vences M. 2017. Phylotranscriptomic consolidation of the jawed vertebrate timetree. *Nature Ecology & Evolution* **1:** 1370-1378.

Jared C, Navas CA, Toledo RC. 1999. An appreciation of the physiology and morphology and physiology of caecilians (Amphibia: Gymnophiona). *Comparative Biochemistry and Physiology A* **123:** 313–328.

Jared C, Mailho-Fontana PL, Marques-Porto R, Sciani JM, Pimenta DC, Brodie EDJ, Antoniazzi MM. 2018. Skin gland concentrations adapted to different evolutionary pressures in the head and posterior regions of the caecilian *Siphonops annulatus*. *Scientific Reports* **8:** 1-7.

Jenkins FA, Walsh DM. 1993. An Early Jurassic caecilian with limbs. *Nature* **365:** 246–250.

Jenkins FA, Walsh DM, Carroll RL. 2007. Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic, *Bulletin of the Museum of Comparative Zoology* **158:** 285-365.

Kamei RG, San Mauro D, Gower DJ, Bocxlaer IV, Sherrat E, Thomas A, Babu S, Bossuyt F, Wilkinson M, Biju SD. 2012. Discovery of a new family of amphibians from northeast India with ancient links to Africa. *Proceedings Biological Sciences* **279:** 2396–2401.

Kozlowski J, Gawelczyk AT. 2002. Why Are Species' Body Size Distributions Usually Skewed to the Right? *Functional Ecology* **16:** 419–32.

Laurin M, Lapauze O, Marjanović D. 2019. What do ossification sequences tell us about the origin of extant amphibians? bioRxiv 352609, ver. 4 peer-reviewed by PCI Paleo. DOI: 10.1101/352609.

Lasseron M, Allain R, Gheerbrant E, Haddoumi H, Jalil NE, Metais G, Rage JC, Vullo R, Zouhi S. 2019. New data on the microvertebrate fauna from the Upper Jurassic or lowest Cretaceous of Ksar Metlili (Anoual Syncline, eastern Morocco). *Geological Magazine* **157:** 367-392.

Laurin M, Arntzen JW, Báez AM, Bauer AM, Damiani R, Evans SE, Kupfer A, Larson A, Marjanović D, Müller H, Olsson L, Rage JC, Walsh D. 2020. Lissamphibia. In: De Queiroz K, Cantino PD, Gauthier JA, eds. *Phylonyms: An Implementation of PhyloCode*. Boca Raton: CRC Press, 755-760.

Lucas SG, Heckert AB, Tanner LH. 2005. Arizona's Jurassic fossil vertebrates and the age of the Glen Canyon Group. *New Mex Mus Nat Hist Sci Bull* **29:** 94-103.

Maddin HC. 2011. Deciphering morphological variation in the braincase of caecilian amphibians (gymnophiona). *Journal of Morphology* **272:** 850-871.

Maddin HC, Jenkins FA, Anderson JS. 2012. The braincase of *Eocaecilia micropodia* (Lissamphibia, Gymnophiona) and the origin of caecilians. *PLoS ONE* **7:** 1-12.

Maddin HC, Venczel M, Gardner JD, Rage JC. 2013. Micro-computed tomography study of a three-dimensionally preserved neurocranium of Albanerpeton (Lissamphibia, Albanerpetontidae) from the Pliocene of Hungary. *J Vertebr Paleontol* **33:** 568–587.

Marjanović D, Laurin M. 2007. Fossils, molecules, divergence times, and the origin of lissamphibians. *Systematic Biology* **56:** 369-388.

Marjanović D, Laurin M. 2008a. A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians. *Contributions to Zoology* **77:** 149-199.

Marjanović D, Laurin M. 2008b. Assessing confidence intervals for stratigraphic ranges of higher taxa: the case of Lissamphibia. *Acta Palaeont Pol* **53:** 413–432. 10.4202/app.2008.0305.

Marjanović D, Laurin M. 2009. The origin(s) of modern amphibians: a commentary. *Evolutionary Biology* **36:** 336–338.

Marjanović D, Laurin M. 2013. The origin(s) of extant amphibians: a review with emphasis on the "lepospondyl hypothesis". *Geodiversitas* **35:** 207–72.

Marjanović D, Laurin M. 2019. Phylogeny of Paleozoic limbed vertebrates reassessed through revision and expansion of the largest published relevant data matrix. *PeerJ* 6:e5565. 10.7717/peerj.5565.

Marsh AD, Rowe T, Simonetti A, Stockli D, Stockli L. 2015. Preliminary U-Pb detrital zircon dates from the Kayenta Formation of Arizona. In: Sankey J, Biewer J, eds. *Western Association of Vertebrate Paleontology Annual Meeting: Program with Abstracts.* Turlock: California Digital Library, 10.

Müller H. 2006. Ontogeny of the skull, lower jaw, and hyobranchial skeleton of *Hypogeophis rostratus* (Amphibia: Gymnophiona: Caeciliidae) revisited. *Journal of Morphology* **267:** 968-986.

Nussbaum RA. 1983. The evolution of a unique dual jaw-closing mechanism in caecilians (Amphibia: Gymnophiona) and its bearing on caecilian ancestry. *Journal of Zoology* **199:** 545-554.

Pardo JD, Small BJ, Huttenlocker AK. 2017. Stem caecilian from the Triassic of Colorado sheds light on the origins of Lissamphibia. *Proceedings of the National Academy of Sciences of the United States of America* **114:** 1-7.

Parham JF, Donoghue PCJ, Bell CJ, Calway TD, Head JJ, Holroyd PA, Inoue JG, Irmis RB, Joyce WG, Ksepka DT, Patané JSL, Smith ND, Tarver JE, Van Tuinen M, Yang Z, Angielczyk KD, Greenwood J, Hipsley CA, Jacobs L, Makovicky PJ, Müller J, Smith KT, Theodor JM, Warnock, RCM, Benton MJ. 2012. Best practices for justifying fossil calibrations. *Systematic Biology* **61:** 346-359.

Peterhans JCP, Wrangham RW, Carter ML, Hauser MD. 1993. A contribution to tropical rain forest taphonomy: retrieval and documentation of chimpanzee remains from Kibale Forest, Uganda. *Journal of Human Evolution* **25:** 485–514.

Pyron RA. 2010. A likelihood method for assessing molecular divergence time estimates and the placement of fossil calibrations. *Systematic Biology* **59:** 185-194.

Pyron RA. 2011. Divergence Time Estimation Using Fossils as Terminal Taxa and the Origins of Lissamphibia. *Systematic Biology* **60:** 466-481.

Pyron RA, Wiens JJ. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians *Molecular Phylogenetics and Evolution* **61:** 543-583.

Pyron RA. 2014. Biogeographic Analysis Reveals Ancient Continental Vicariance and Recent Oceanic Dispersal in Amphibians. *Systematic Biology* **63:** 779-797.

Rage JC. 1991. Gymnophionan Amphibia from the Early Paleocene (Santa Lucia Formation) of Tiupampa (Bolivia): the oldest known Gymnophiona. *Revista Tecnica de YPFB* **12:** 3-4.

Rage JC, Pickford M. 2011. Discovery of a Gymnophionan skull (?Caeciliidae, Amphibia) in the Early Miocene of Uganda. *Geo-Pal Uganda* **4:** 1-9.

Renous S, Gasc JP. 1989. Body and Vertebral Proportions in Gymnophiona (Amphibia): Diversity of Morphological Types. *Copeia* **1989:** 837-847.

Roelants K, Gower DJ, Wilkinson M, Loader SP, Biju SD, Guillaume K, Bossuyt F. 2007. Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences* **104:** 887-892.

Ruta M, Coates I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. *Journal of Systematic Palaeontology* **5:** 69-122.

San Mauro D. 2010. A multilocus timescale for the origin of extant amphibians. *Molecular Phylogenetic Evolution* **56:** 554-561.

San Mauro D, Gower DJ, Muller H, Loader SP, Zardoya R, Nussbaum RA, Wilkinson M. 2014. Life-history evolution and mitogenomic phylogeny of caecilian amphibians. *Molecular Phylogenetic Evolution* **73:** 177-189.

Schoch RR. 2008. A New Stereospondyl from the German Middle Triassic, and the Origin of the Metoposauridae. *Zoological Journal of the Linnean Society* **152:** 79–113.

Schoch RR, Milner AR. 2004. Structure and implications of theories on the origin of lissamphibians. In: Arratia G, Wilson MVH, Cloutier R, eds. *Recent Advances in the Origin and Early Radiation of Vertebrates*. Munich: Dr Friedrich Pfeil Verlag, 345-377.

Schrank E. 1990. Palynology of the clastic Cretaceous sediments between Dongola and Wadi Muqaddam, northern Sudan. *Berliner Geowissenschaftliche Abhandlungen, Reihe A* **120:** 149-168.

Sherrat E, Gower DJ, Klingerberg CP, Wilkinson M. 2014. Evolution of Cranial Shape in Caecilians (Amphibia: Gymnophiona). *Evolutionary Biology* **41:** 528-545.

Sigogneau-Russel D, Monbaron M, Kaenel ED. 1990. Nouvelles Données sur le Gisement à Mammifères mésozoïques du Haut-Atlas marocain. *Geobios* **23:** 461-483.

Szostakiwskyj M, Pardo JD, Anderson JS. 2015. Micro-CT Study of *Rhynchonkos stovalli* (Lepospondyli, Recumbirostra), with Description of Two New Genera. *PLoS ONE* **10:** e0127307.doi:10.1371/journal.pone.0127307

Tappen M. 1994. Bone weathering in the Tropical Rain Forest. *Journal of Archaeological Science* **21:** 667-673.

Taylor EH. 1968. *The caecilians of the World*. Lawrence: University of Kansas Press.

Taylor EH. 1977. Comparative anatomy of caecilian anterior vertebrae. *The University of Kansas Science Bulletin* **51:** 209-231.

Trueb L, Cloutier R. 1991. A Phylogenetic Investigation of the Inter and Intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In: Schultze HP, Trueb L, eds. *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Ithaca: Cornell University Press, 233- 313.

Vallin G, Laurin M. 2004. Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology* **24:** 56-72.

Van Dijk DE. 1995. African fossil Lissamphibia. *Palaeontologica Africana* **32:** 39-43.

Wake MH, Wurst GZ. 1979. Tooth crown morphology in caecilians (Amphibia: Gymnophiona). *Journal of Morphology* **159:** 331-341.

Wake MH. 1980. Morphometrics of the skeleton of *Dermophis mexicanus* (Amphibia: Gymnophiona). Part I. The vertebrae, with comparisons to other species. *Journal of Morphology* **165:** 117-130.

Wake MH, Hanken J. 1982. Development of the skull of *Dermophis mexicanus* (amphibia: Gymnophiona), with comments on skull kinesis and amphibian relationships. *Journal of Morphology* **173:** 203-223.

Wake TA, Wake MH, Lesure RG. 1999. First Quaternary Fossil Record of Caecilians from a Mexican Archaeological Site. *Quaternary Research* **52:** 138-140.

Wellstead CF. 1991. Taxonomic revision of the Lysorophia, Permo-Carboniferous lepospondyl amphibians. *Bulletin of the American Museum of Natural History* **209:** 1-90.

Werdelin L. 2010. Chronology of Neogene Mammal localities. In Werdelin L, Sanders WJ, eds. *Cenozoic mammals of Africa*. Berkeley: University of California Press, 27-43.

Werner C. 1994. Der erste Nachweis von Gymnophionen (Amphibia) in der Kreide (Wadi-Milk-Formation, Sudan). Neues Jahrbuch fur Geologie und Palaontologie **10:** 633-640.

Wilkinson M. 1991. Adult tooth crown morphology in the Typhlonectidae (Amphibia: Gymnophiona). *Journal of Zoological Systematics and Evolutionary Research* **29:** 304-311.

Wilkinson M, Nussbaum RA. 2006. Caecilian Phylogeny and Classification. In: Exbrayat JM, ed. *Reproductive Biology and Phylogeny of Gymnophiona (Caecilians).* Enfield: Science Publishers, 39-78.

Wilkinson M, San Mauro D, Sherratt E, Gower DJ. 2011. A nine-family classification of caecilians (Amphibia: Gymnophiona). *Zootaxa* **2874:** 41–64.

Wilkinson M, Kupfer A, Marques-Porto R, Jeffkins H, Antoniazzi MM, Jared C. 2008. One hundred million years of skin feeding? Extended parental care in a Neotropical caecilian (Amphibia: Gymnophiona*). Biology Letters* **4:** 358–361.

Yates AM, Warren A. 2000. The Phylogeny of the 'Higher' Temnospondyls (Vertebrata: Choanata) and Its Implications for the Monophyly and Origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128:** 77-121.

Zhang P, Zhou H, Liu YF, Qu LH. 2005. Mitogenomic perspectives on the origin and phylogeny of living amphibians. *Systematic Biology* **54:** 391-400.

Zhang P, Wake MH. 2009. A mitogenomic perspective on the phylogeny and biogeography of living caecilians (Amphibia: Gymnophiona), *Molecular Phylogenetic Evolution* **53:** 479-491.

Figures

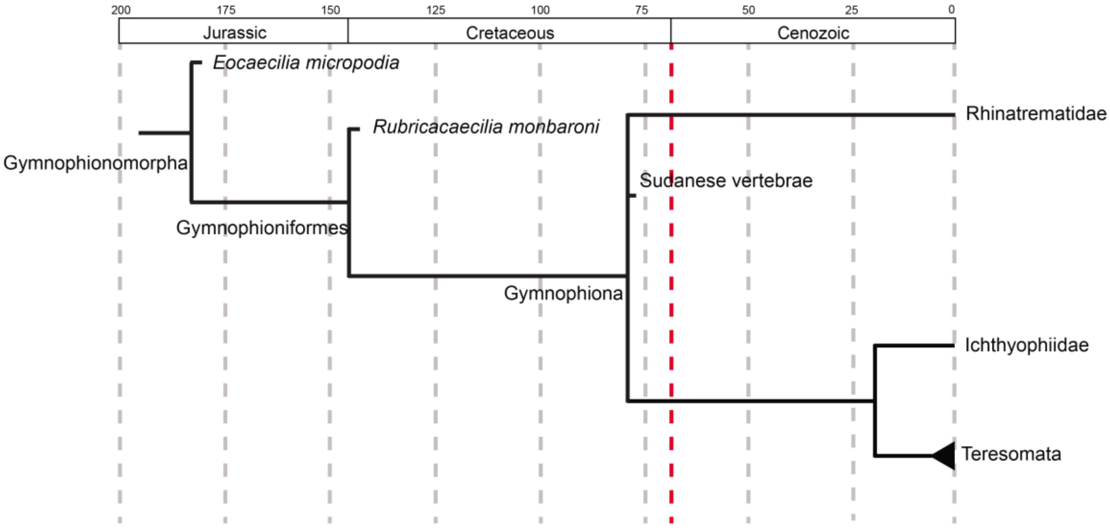

Fig. 1: Time-calibrated phylogeny of Gymnophionomorpha, including stem lineages plus the crown-group Gymnophiona, compiled from Wilkinson et al. (2011) and Evans & Sigogneau-Russel (2001). Red doted lines indicate K-Pg boundary.

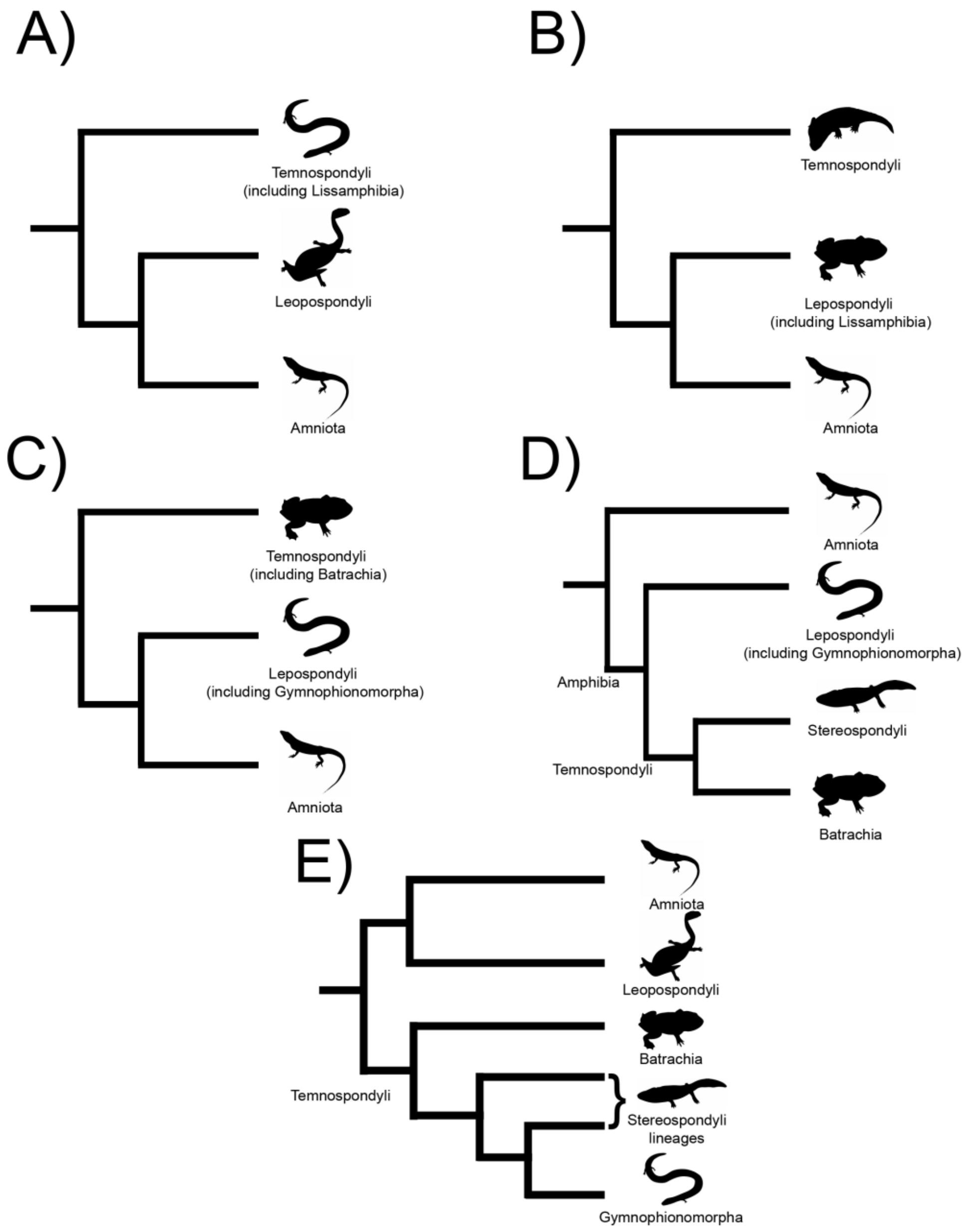

Fig. 2: The different proposals for the phylogenetic relationships of Lissamphibia, based on Marjanović & Laurin (2008a), Laurin et al. (2019) and Pardo et al. (2017). A) temnospondyl hypothesis. B) Lepospondyl hypothesis. C) One of the examples of polyphyly hypothesis. D) Alternative topology also related to polyphyly hypothesis. E) Topology recovered 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.

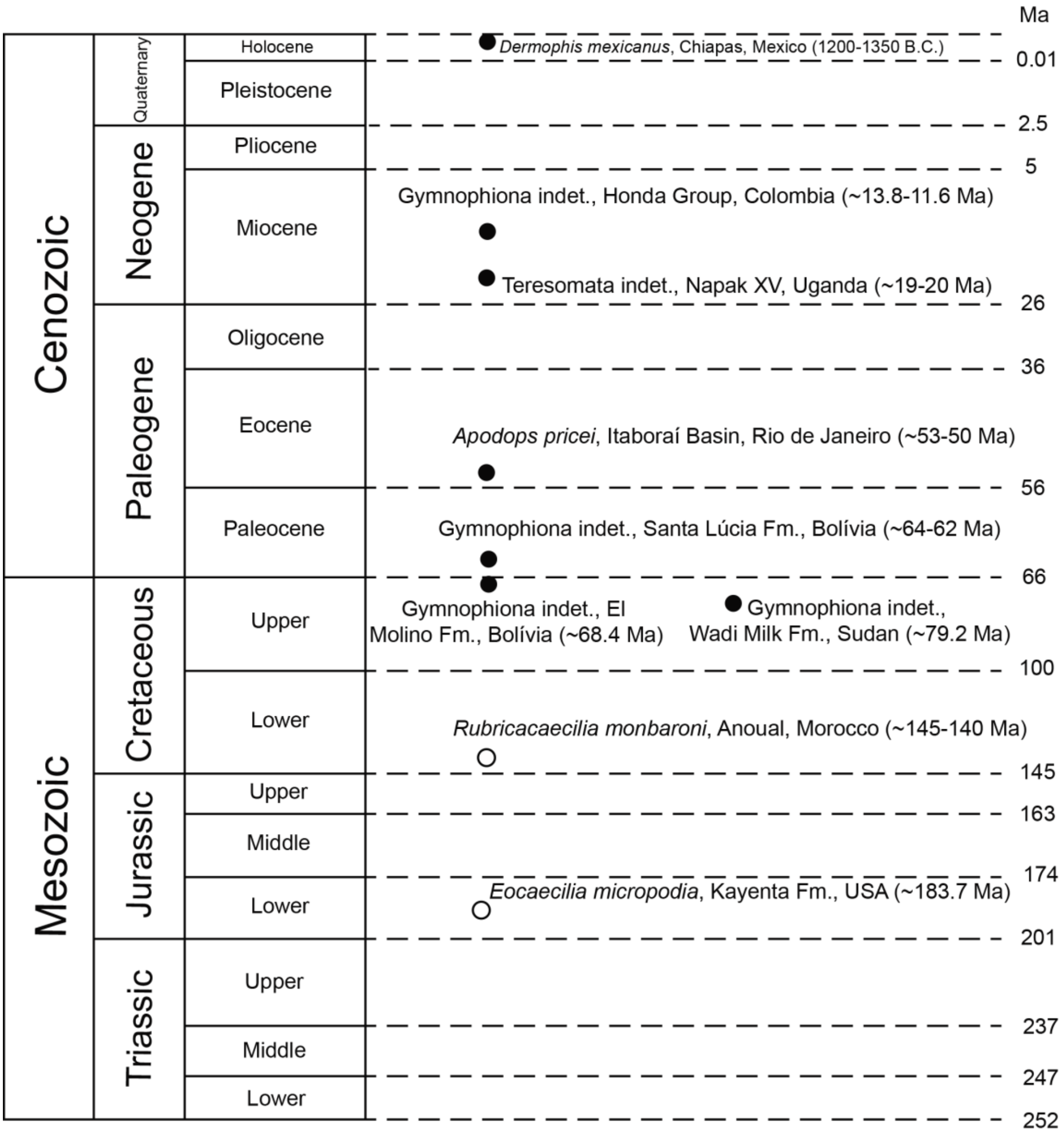

Fig. 3: The fossil record of Gymnophionomorpha through geological time. Black circles indicate crown-group taxa, while white ones indicate stem-lineages.

Fig. 4: Distribution of extant caecilians, along with the locations where fossils attributed to the group were found. Orange marks indicate stem lineages, while white ones correspond to fossils assigned to 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).

doi:10.20944/preprints202006.0264.v1

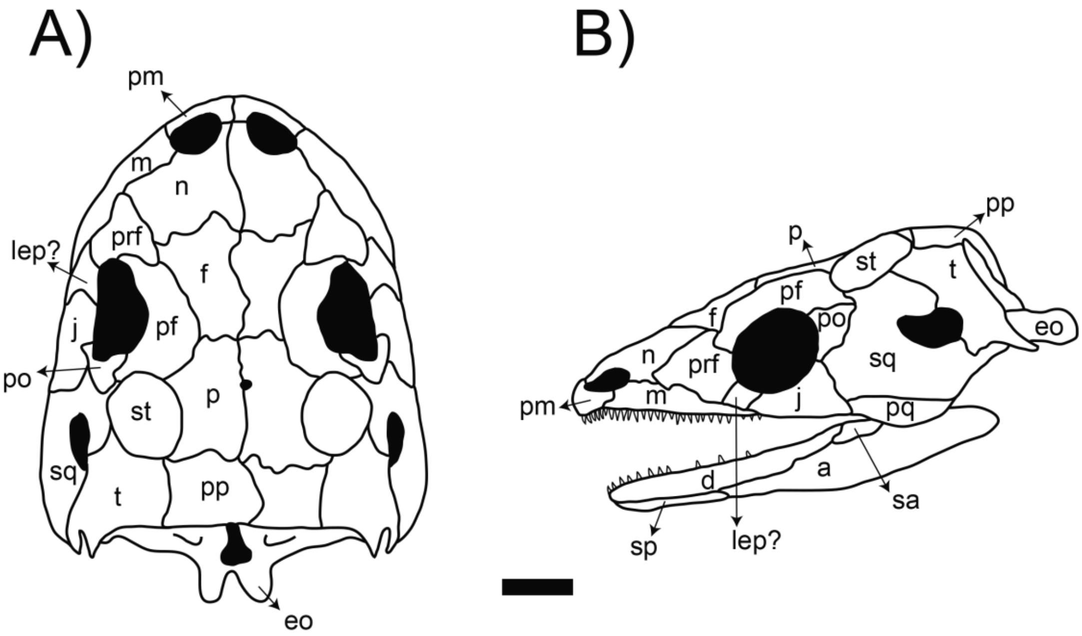

Fig. 5: Reconstructions of the *C. jenkinsi* skulls in dorsal (A) and lateral (B) views. Redraw from Pardo et al. (2017). Abbreviations: a, angular; ch, choana; d, dentary; dt, dorsal table; eo, exoccipital; f, frontal; j, jugal; lep, lateral exposure of palatine; m, maxilla; mp, maxillopalatine; n, 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; rpp, rostral process of parasphenoid; sa, surangular; sp, splenial; sph, sphenethmoid; spm, septomaxilla; sq, squamosal; st-q, stapes-quadrate; st, supratemporal; t, tabular; to, tooth. Scale bar = 5 mm.

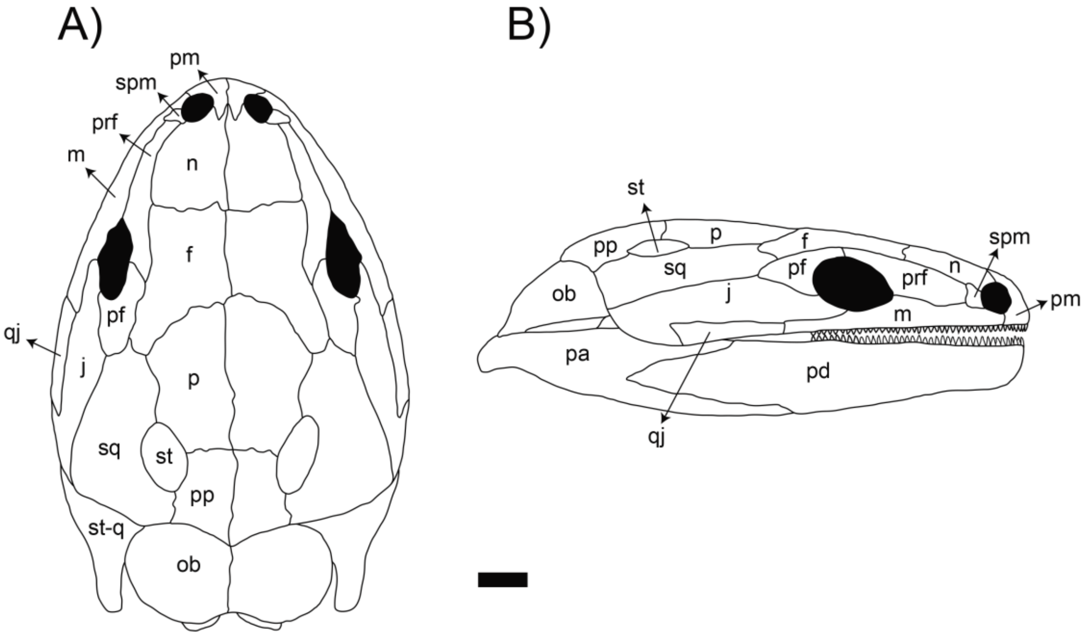

Fig. 6: Reconstruction of *E. micropodia* skull in dorsal (A) and lateral (B) views. Redraw from Jenkins et al. (2007). See figure 5 for abbreviations. Scale bar = 1 mm.

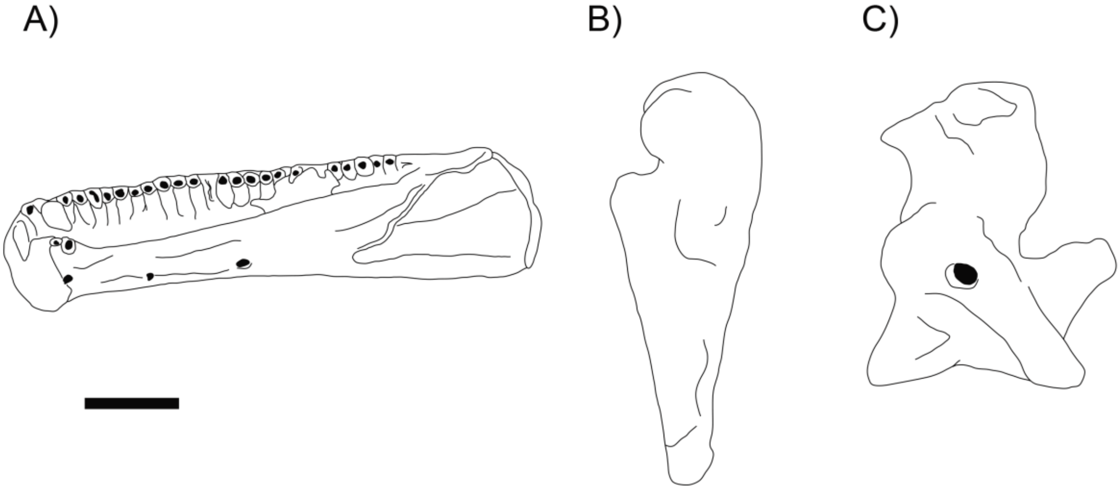

Fig. 7: Reconstructions of *R. monbaroni* holotype (MCM 171), a right pseudodentary in lingual view (A), the proximal head of a left femur (B) tentatively associated with the species (MCM 3) and MCM 175, an atlas in right lateral view (C). Redraw from Evans & Sigogneau-Russel (2001). Scale bar = 1 mm.

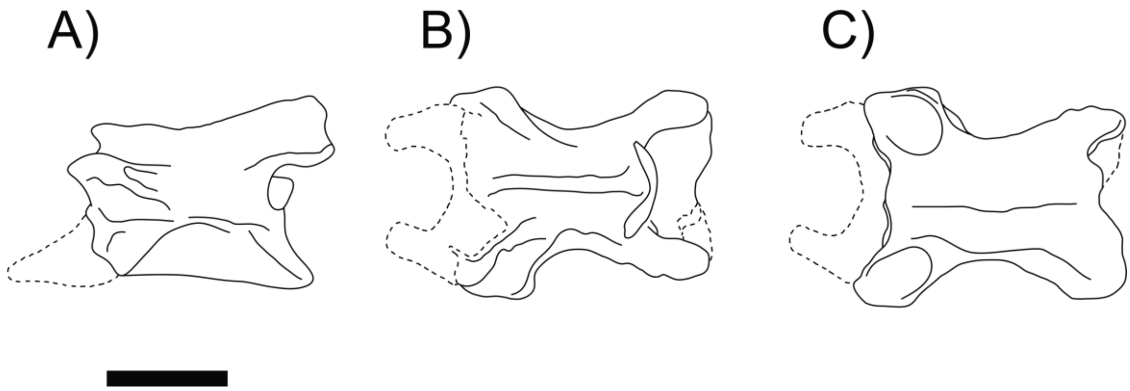

Fig. 8: Lateral (A), ventral (B) and dorsal (C) views of DGM 551, a precloacal vertebra assigned to *A. pricei*. Missing parts were marked with a dotted line. Redraw from Estes & Wake (1972). Scale bar = 1 mm.

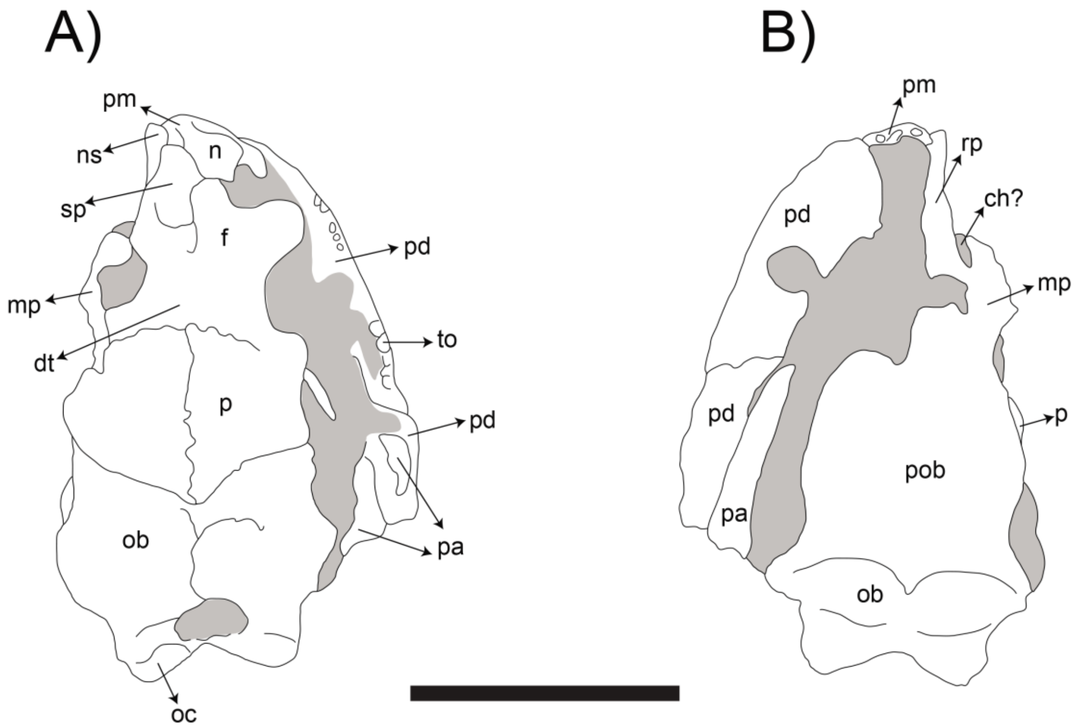

Fig. 9: Dorsal (A) and ventral (B) views of Nap XV 148’08, a Teresomata indet. Areas covered by rock are indicated in grey. Redraw from Rage & Pickford (2011) and Gardner & Rage (2016). See figure 5 for abbreviations. Scale bar = 1 cm.