

Rodolfo Otávio dos Santos

Descrição morfológica e análise filogenética de
uma cecília fóssil (Lissamphibia,
Gymnophiona), da Bacia de Taubaté, região do
Vale do Paraíba, São Paulo

Morphological description and phylogenetic
analysis of a fossil caecilian (Lissamphibia,
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For Ana and for my family, especially my grandfather

Writing is perhaps the greatest of human inventions,
binding together people who never knew each other,
citizens of distant epochs. Books break the shackles of time.
A book is proof that humans are capable of working magic.

(Carl Sagan, 1934–1996, in *Cosmos*, 1980)

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Abstract

The Gymnophiona clade, usually considered as the least known group of living tetrapods, includes animals popularly called caecilians, characterized by their well-ossified skull with reduced or even absent eyes, an elongated and annulate body lacking limbs. The clade is moderately diversified, and currently 214 species distributed in tropical regions of South and Central America, Africa and Southeast Asia are known. Its fossil record is particularly scarce, including only 3 named taxa (*Eocaecilia micropodia*, *Rubricacaecilia monbaroni*, and *Apodops pricei*) and other fragmented materials, mostly vertebrae, whose taxonomic attribution remains undetermined. In this work, in addition to a review of the caecilian fossil record, a new specimen of Gymnophiona based on a fossil material, DGM 1462-R, found in deposits of the Tremembé Formation, Taubaté Basin (Oligocene), was described and phylogenetically positioned. DGM 1462-R shares unique features with caecilians, such as the presence of pseudangular, pseudodontaries, os basale, elongated and limbless bodies, vertebrae amphicoelous and with well-developed parasphenes. DGM 1462-R was recovered nested among typhlonectids, a group of caecilians known by their aquatic or semi-aquatic lifestyle. Characteristics shared with at least some of the representatives of Typhlonectidae include the presence of a constriction prior to postzygapophysis at the neural arch of the atlas, elongated vertebrae, a well-developed ventral ridge in the parasphenes, low nuchal crests, ribs expanded anteroventrally and with elongated capitulum. DGM 1462-R represents the first fossil of a crown-Gymnophiona included in a phylogeny with other living taxa, and consequently, the first Typhlonectidae fossil ever described. Additionally, it represents the first known caecilian for the Oligocene and the second record of an amphibian for the Taubaté Basin.

Keywords: Lissamphibia; Gymnophiona; Typhlonectidae, Taubaté Basin; Oligocene, Phylogenetic Systematics

Resumo

O clado Gymnophiona, frequentemente considerado como o menos conhecido dentre todos os táxons de tetrápodes vivos, inclui animais popularmente chamados de cecílias, caracterizadas pelo crânio bem ossificado e com olhos reduzidos ou até mesmo ausentes, corpo alongado e anulado, e sem membros. É um clado moderadamente diverso, e atualmente são conhecidas 214 espécies distribuídas nas regiões tropicais das Américas do Sul e Central, África e Sudeste Asiático. Seu registro fóssil é particularmente escasso, incluindo apenas 3 táxons nomeados (*Eocaecilia micropodia*, *Rubricacaecilia monbaroni*, e *Apodops pricei*) além de outros materiais fragmentados, em sua maioria vértebras, cuja atribuição taxonômica permanece como indeterminada. Neste trabalho, além de uma revisão do registro fóssil de cecílias, um novo espécime de Gymnophiona fóssil, DGM 1462-R, encontrado em depósitos da Formação Tremembé, Bacia de Taubaté (Oligoceno), foi descrito e filogeneticamente posicionado. DGM 1462-R compartilha feições únicas com cecílias, tais como a presença de pseudangular, pseudodentário, os basale, o corpo alongado e sem membros, vértebras anficélicas e com parasfenos bem desenvolvidos. DGM 1462-R foi recuperado entre os typhlonectídeos, grupo de cecílias caracterizado pelos seus hábitos aquáticos ou semiaquáticos. Características compartilhadas com ao menos algum dos representantes de Typhlonectidae incluem a presença de constrição anterior à pós-zigapófise no arco neural do atlas, vértebras alongadas, cume ventral nos parasfenos bem desenvolvido, crista nugal baixa, costelas expandidas anteroventralmente e com capitulum alongado. DGM 1462-R representa o primeiro fóssil de uma crown-Gymnophiona incluso em uma filogenia junto às demais espécies viventes, e conseqüentemente o primeiro fóssil de Typhlonectidae já descrito. Adicionalmente, representa a primeira cecília conhecida para o Oligoceno e o segundo registro de um anfíbio para a Bacia de Taubaté.

Palavras-chave: Lissamphibia; Gymnophiona; Typhlonectidae, Bacia de Taubaté; Oligocene, Sistemática Filogenética

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1. Introduction

The modern amphibians form the only group of living non-amniotic tetrapods, known as Lissamphibia, sharing characteristics like the presence of pedicellate teeth and the capacity to use the surface of skin, rich in different kinds of glands, for gas exchange (Carroll, 2009). Three subgroups belong to the Lissamphibia – the Anura (frogs and toads), Urodela (salamanders), and Gymnophiona (caecilians) – and each one exhibits different lifestyles in a variety of habitats, such as terrestrial, fossorial and freshwater environments, being widely distributed in temperate and mainly tropical areas (Duellman & Trueb, 1994). Among lissamphibians, the clade Gymnophiona (Figure 1) is the one with the smallest number of species described – approximately 210 (Frost, 2018) – and the least known in aspects of its systematics and ecology (Nussbaum & Wilkinson, 1989).



Figure 1: Representatives of caecilian species found in Brazil. A) *Caecilia tentaculata*. B) *Rhinatremas bivittatus*. C) *Siphonops paulensis*. D) *Typhlonectes compressicauda*. Modified from Borges-Nojosa *et al.* (2016), Maciel (2009) and Maciel (2016).

Despite the lack of consensus on Lissamphian monophyly, there is little doubt that extant caecilians form a natural group (Figure 6), supported by many unambiguous synapomorphies, including both molecular and morphological (Frost *et al.*, 2006; Marjanovic & Laurin, 2007). Popularly called caecilians, they are mainly recognizable

by their elongate limbless, serpentiform body, vestigial eyes, and smooth skin (Wilkinson *et al.*, 2011). Uniquely derived features include a compact and well-ossified skull, double jaw closing mechanism, the presence in the nostril of a pair of sensitive organs called tentacles, an atlas without a *tuberculum interglenoideum*, an elongated and annulated body, an eversible phallus in males and the absence of scapular and pelvic girdles (Wilkinson & Nussbaum, 2006).

Many of these features were interpreted as adaptations for excavation and were somewhat related to a fossorial behavior (Duellman & Trueb, 1994; Bardua *et al.*, 2019). Despite this generalization, the morphological diversity in the clade suggests the occurrence of secondary adaptations towards different lifestyles and habitats, including wet soils and aquatic environment (well known for the Typhlonectidae family) or tropical forest litter (Taylor, 1968; Jared *et al.*, 1999).

The term Gymnophiona, instead of Apoda, is traditionally used to refer to the crown group (e.g. Cannatella & Hills, 1993; Frost *et al.*, 2006; Marjanovic & Laurin, 2008a; Wilkinson *et al.*, 2011), mainly because the former name is already well established while the latter is commonly used to designate other animals, such as the moth genus *Apoda* Haworth 1809 (Wilkinson & Nussbaum, 2006). Despite the scarcity of fossil caecilians, the few that are known are of significant importance (see chapter below). Caecilian total group, including these stem lineages plus the crown group, corresponds to the clade Gymnophionomorpha (Marjanović & Laurin, 2008a). This clade comprises all species more closely related to the crown Gymnophiona than to Batrachia, while Gymnophiona includes the last common ancestor of *Caecilia tentaculata* and *Rhinatrema bivittatum* all its the descendants (Marjanovic & Laurin, 2008a).

1.1. Short Historical Background

In the 10th edition of the famous Systema Naturae, Carl von Linnaeus named two caecilian species: *Caecilia tentaculata* and *Caecilia i glutinosa* (currently known as *Ichthyophis glutinosus*). The name Caecilia comes from the Latin *caecus*, meaning “blind”, a reference to the reduced or possibly absent eyes of these animals, while the epithet refers to the tentacles, their exclusive sensory organs. The clade is also called Gymnophiona, a term formed by the combination of Greek words “*gymnos*” (naked) and *ophioneos* (similar to snake), a reference to the snake-like body shape that lack scales

(although dermal scales are present in some caecilian species). The name Apoda, from the Greek “A” (no) and “*podós*” (foot) is also commonly used to designate caecilians.

Prior to Edward Taylor's seminal works, in 1968 and 1969, caecilian diversity was considered low and all species were assigned to only one family – Caeciliidae – since the group was neglected by most herpetologists (Nussbaum & Wilkinson, 1989). In his studies, Taylor demonstrated that the morphological and behavior diversity of caecilians were highly underestimated, a fact reflected in his new proposal for the classification of Gymnophiona, in which three new families were recognized: Ichthyophidae, Scolecomorphidae and Typhlonectidae (Taylor, 1968; 1969).

Despite its limited diversity, recent works have shown that caecilians exhibit great morphological complexity and a wide variety of lifestyles, habitats and reproductive strategies (Wake, 2006). Currently, with modern techniques as CT-Scan and phylogenomics, knowledge about caecilian morphology and phylogenetic relationships advanced substantially (e.g. Wilkinson *et al.*, 2011; San Mauro *et al.*, 2014).

1.2. Gymnophiona General Morphology

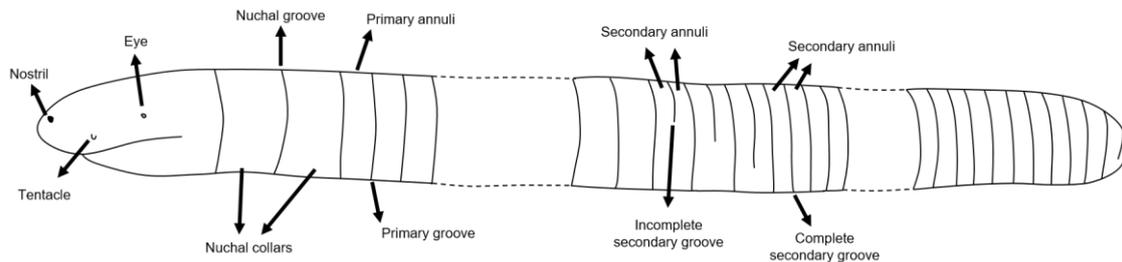


Figure 2: Schematic representation of a caecilian, showing some anatomic structures commonly used for its identification. Modified from Lynch (1999).

1.2.1. External morphology

Gymnophionans can be easily recognized due to the adaptations required by their predominantly fossorial way of life (Duellmann & Trueb, 1994). Typical characteristics of caecilians include an elongated and annulate body, the lack of limbs and girdles, the presence of tentacles, reduced or completely absent eyes, and a compact skull (Figure 2). However, despite this rather simple diagnosable bauplan, caecilians are hard to identify at the specific level for which correct identifications are hampered by their considerably conservative external morphology (Wilkinson & Nussbaum, 2006).

In caecilians, the mouth position can be terminal or subterminal, and this feature varies according to the lifestyle of each species. Therefore, a rostrum with a strong anterior projection, ideal for excavation, and a mouth positioned more posteriorly, is generally expected in taxa that actively dig (Nussbaum, 1983). Such features, along with the relative position of tentacles in relation to the eyes and nostril, the type of annulation found in the body, and the shape and number of annular scales, constitute some of the few external morphological characteristics used for taxonomic purposes (e.g. Nussbaum, 1979; Wilkinson, 1997; Lynch, 1999).

The occurrence of annuli in the body (Figure 2), a feature related to body segmentation, is typical within Gymnophiona. At the posterior region of the skull, caecilians bear nuchal collars, usually larger than other adjacent annuli. These collars are composed by a maximum of two annuli and delimited anteroposteriorly by grooves that may, or may not, surround the body (Taylor, 1968). The primary annuli are similar to the nuchal collars, but lightly narrower, being limited by grooves that, depending on the species, entirely surround the body (Nussbaum & Wilkinson, 1989). In the posterior portion of the body, primary rings can be divided by a secondary groove, forming two secondary annuli and, in addition, in some taxa the presence of tertiary grooves subdivides each secondary annulus in two tertiary annuli (Lynch, 1999).

Unlike other lissamphibians, many caecilians bear scales organized in rows, inside skin folds or pockets, and therefore inconspicuous externally, a characteristic that may also be related to their burrowing behavior (Taylor, 1972). These scales are composed by two layers, one basal that is formed by collagenous fibers and another more superficial and mineralized (Jared *et al.*, 1999). Patterns of scalation are correlated with body annulation, and therefore are also known to be phylogenetically informative. However, characters related to body annulation have to be viewed with caution, since they faced criticisms related to misunderstandings about scale ontogeny, homology, and intraspecific variation (see Nussbaum & Wilkinson, 1989).

The lack of a true tail is considered a derived feature in caecilians, and typical of the Teresomata subgroup (Wilkinson & Nussbaum, 2006). A true tail (Figure 3) can be defined as a postcloacal region with internal and external segmentation (namely, the presence of vertebrae and annuli, respectively) and the absence of internal flexures of the *m. rectus lateralis* (Nussbaum & Naylor, 1982). The true tail is characteristic of rhinatrematids and ichthyophids (Wilkinson, 1992; 1997). However, some teresomatans

exhibit a post-cloacal extension known as pseudotail, not homologous with a true tail (Nussbaum & Wilkinson, 1989).

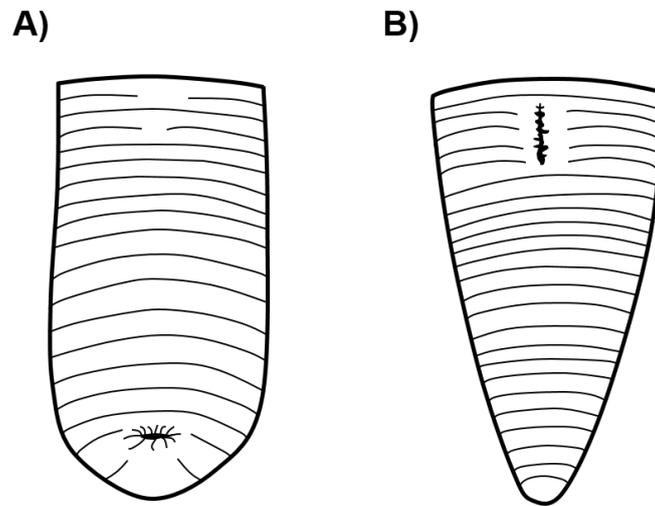


Figure 3: Ventral view of a caecilian posterior region. A) The typical teresomatan body terminus. B) A true tail from the rhinatrematid *Epicrionops bicolor*. Modified from Lynch (1999).

1.2.2. Skull

Due to the gradual and frequent events of fusion and/or loss of bones, the skull of gymnophionans is significantly different from the other two lissamphibian groups (Duellmann & Trueb, 1994). Examples of unique cranial ossifications, formed through the fusion of adjacent bones, include the os basale (originated by the fusion of exoccipitals, opisthotics, prootics, basisphenoid and parasphenoid) and the maxillopalatine (the result of lacrimals, maxillas and nasals fusion) (Müller *et al.*, 2005; Müller, 2006), while examples of complete loss of bones comprises the post-parietal and supratemporal (Jenkins *et al.*, 2007).

Two patterns of cranial bone arrangement that evolved independently in some lineages are promptly recognizable within caecilians (Figure 4). The first, called Stegokrotaphy, is typical of species that dig actively and is characterized by the presence of a well-ossified skull in which the squamosal and parietals are in contact and cover completely the adductor chambers (Kleinteich *et al.*, 2012). The second pattern, known as Zygokrotaphy, is characterized by a fenestrated temporal region in which the parietals and squamosals remain separated and the adductor muscles are visible externally (e.g. Nussbaum, 1983; Wilkinson & Nussbaum, 1997).

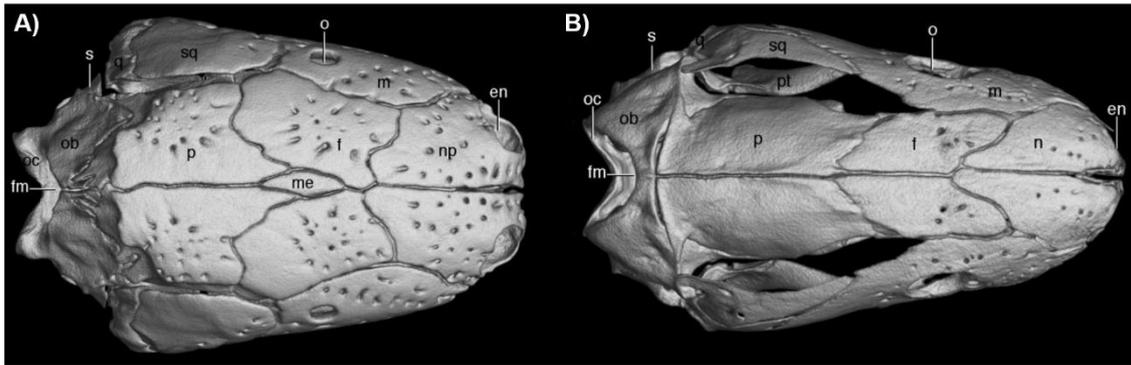


Figure 4: Dorsal view of two caecilian skulls. A) *Caecilia tentaculata*, with its closed skull roof. B) *Rhinatremas bivittatum*, bearing a zygokrotaphic skull. Abbreviations: en: external naris; f: frontal; fm: foramen magnum; m: maxillopalatine; me—mesethmoid; n: nasal; np: nasopremaxilla; o: orbit; ob: os basale; oc: occipital condyle; p: parietal; pt – pterygoid; q: quadrate; s: stapes; sq: squamosal. Modified from Wilkinson *et al.* (2011).

Recent phylogenetic studies employed successfully characters from the braincase and stapes (Wake, 1993; Wilkinson, 1997; Maddin, 2011; Maddin *et al.*, 2012a, Maddin *et al.*, 2012b). In adult gymnophionans, the braincase is formed by two bony elements: the sphenethmoid and the os basale. The sphenethmoid is located more anteriorly and is composed by a main body and two processes, an anterolateral and a dorsomedial, whereas the os basale lies at the posterior portion of skull, forming the floor, sides, and part of the roof that surrounds the brain (Wake, 1993). In its antotic region, numerous foramina, or a single large foramen, serve as a passage for blood vessels and cranial nerves, and its conformation has significant phylogenetic signal (e.g. Maddin, 2011; Wilkinson *et al.*, 2011).

The lower jaw of modern caecilians is composed by two bones, an anterior pseudodentary, presumably formed by the fusion of dentary, coronoid, splenial and parts of Meckel cartilage, and a posterior pseudangular, the result of the fusion of angular, pre-articular and articular (Pardo *et al.*, 2017). As well as other lissamphibians, gymnophionans bear pedicellate teeth which can be mono or bicuspid (Wake & Wurst, 1979), arranged in two rows, one external and other internal. The latter is sometimes called “splenial row” and is absent in some species (e.g. Wilkinson & Nussbaum, 2006). Tooth morphology (Figure 5) varies interspecifically and also during ontogeny, because the dentition of juveniles of dermatophagous species is highly specialized (Kupfer *et al.*, 2006).

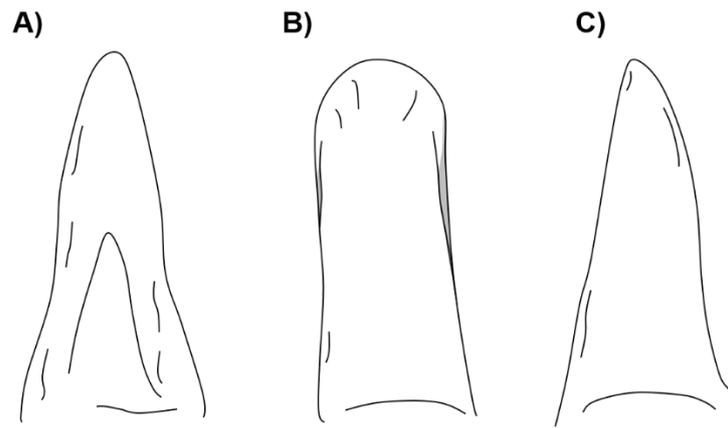


Figure 5: Morphologically distinct adult caecilian tooth crowns in lingual view. A) Bicuspid tooth. B) Anterior spatulate tooth of *Typhlonectes compressicauda* with lateral flanges (in gray). C) Monocuspid conical tooth. Redrawn from Wilkinson (1991).

1.2.3. Postcranium

The caecilian postcranial anatomy is poorly known, and works on this subject are usually limited to descriptions brief and general (e.g. Peter 1894; Taylor, 1977; Renous & Grasc, 1989) or more detailed but focused in one or a small set of species (e.g. Estes & Wake, 1972; Wake, 1980; Wilkinson & Nussbaum, 1997; 1998). Characterized by its elongation and lack of girdles, the postcranial skeleton of caecilians, with the exception of atlas and anteriormost vertebrae, is considered to be quite conservative in most of taxa (e.g. Taylor, 1977; Wake, 1980).

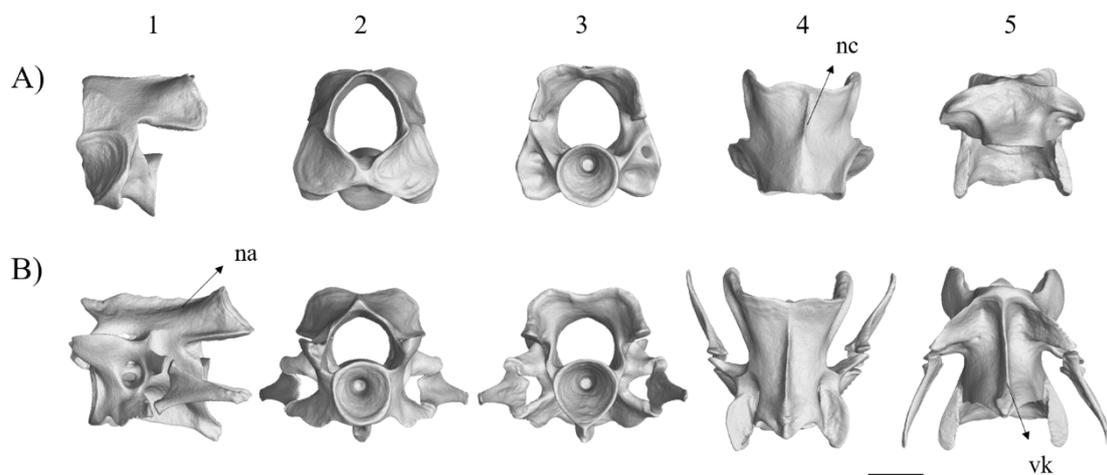


Figure 6: Atlas (row A) and second vertebra (row B) of *Caecilia tentaculata* in lateral (1), anterior (2), posterior (3), dorsal (4), and ventral (5) views. Abbreviations: na: neural arch; nc: nuchal crest; vk: ventral keel. Scale bar = 1 mm.

The number of vertebrae can vary intra and interspecifically, with a maximum of almost 290 (Nussbaum & Naylor, 1982). In the atlas (Figure 6), the most distinctive feature is the lack of *tuberculus interglenoideum* (Evans & Sigogneau-Russell, 2001). The subsequent vertebrae exhibit a morphology typical for caecilians, with an amphicoelous centra medially constricted and with a pronounced ventral keel, wide parasphenes bearing well-developed parapophyses, low and flat neural arches with short neural spines (Estes & Wake, 1972).

1.3. Systematic and Classification of the Gymnophiona

Traditional phylogenetic hypotheses of caecilian affinities (Figure 7) were based only in morphological and ecological characters. More recently, our understanding of caecilian interrelationships improved significantly with the incorporation of molecular data (e.g. Wilkinson, 2003; San Mauro *et al.*, 2004, 2014; Zhang *et al.*, 2005; Zhang & Wake, 2009, San Mauro *et al.*, 2014). These new body of evidence have been seen as pivotal since caecilians are relatively conservative morphologically and rare in scientific collections (e.g. Gower & Wilkinson, 2005; Maciel & Hoogmoed, 2011).

Among the main morphological characters used for a caecilian diagnosis, the coloring pattern, the relative position of tentacles, the fusion or absence of skull bones, count and shape of teeth, the presence of a true tail, the degree of development of the eyes, the phallus, braincase, and anteriormost vertebral morphology, annulation and scalation patterns (Wilkinson & Nussbaum, 2006). In terms of ecological characters, reproductive behaviors (viviparous or oviparous) are the most commonly used characteristics (Wake, 1977).

Most studies treating caecilian affinities rarely include names for suprafamiliar clades, with few exceptions (e.g. Cannatella & Hills, 1993; Wilkinson & Nussbaum, 2006). All caecilians species were originally allocated in a single family, Caeciliidae, by default (Wilkinson *et al.*, 2011), but after the pioneering works developed by Taylor (1968; 1969) new families and higher taxa were recognized. Over time, proposals for the classification of gymnophionans have varied between the more “conservative”, with only three families (e.g. Frost *et al.*, 2006; Pyron & Wiens, 2011) and the more “liberal” schemes, with up to ten families (e.g. Kamei *et al.*, 2012; San Mauro *et al.*, 2014).

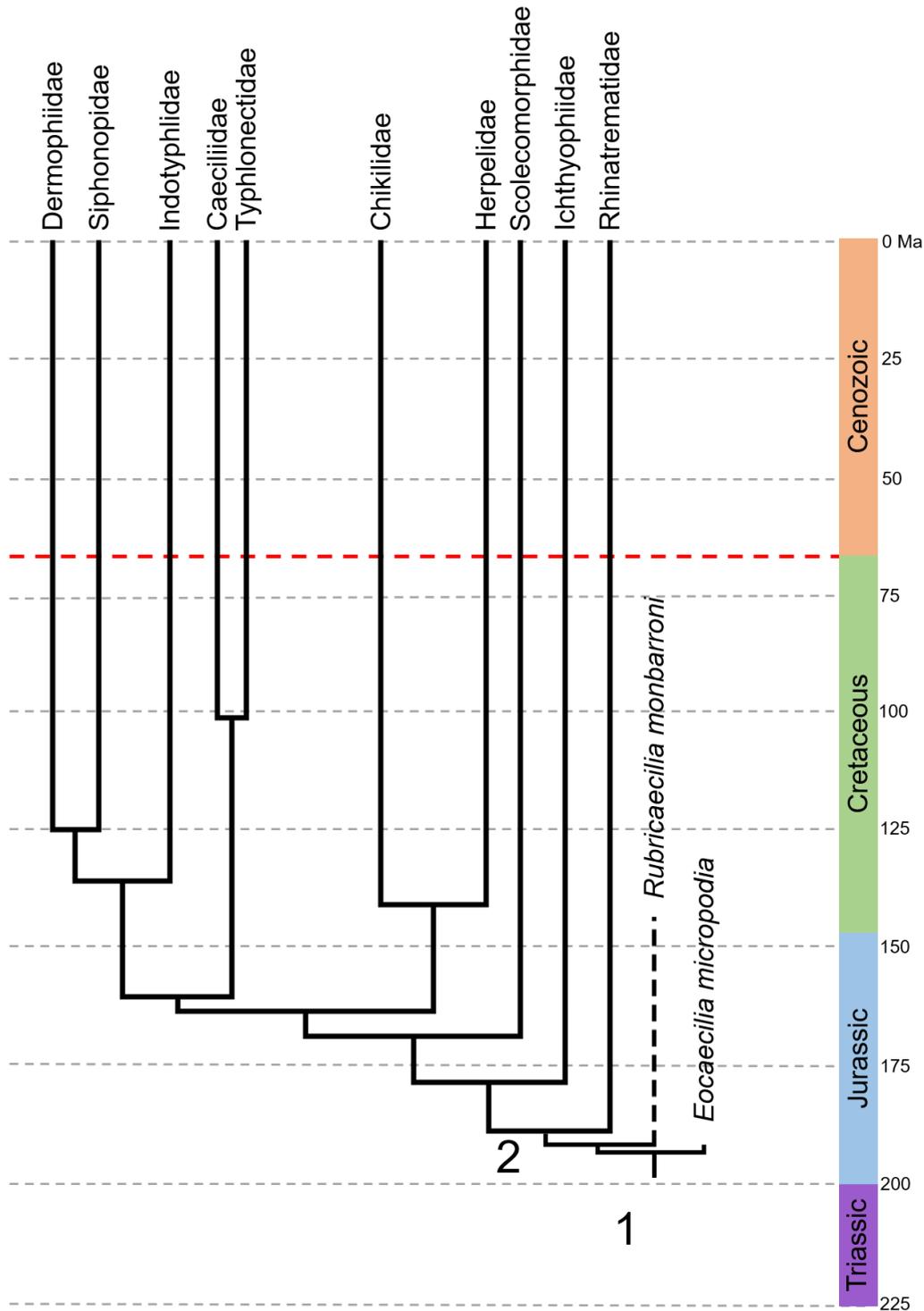


Figure 7: Phylogeny of Gymnophionomorpha (node 1), including stem lineages plus the crown-group (node 2), compiled from Kamei *et al.* (2012); Wilkinson *et al.* (2011) and Evans & Sigogneau-Russell (2001). Red dotted lines indicate K-Pg boundary.

Among recent classifications, “liberal” proposals received more attention, and are currently the most accepted, being supported by both molecular and morphological data (e.g. Wilkinson *et al.*, 2011; Kamei *et al.*, 2012; San Mauro *et al.*, 2014). The consensus for extant species indicates the recognition of ten monophyletic families: Rhinatrematidae

Nussbaum, 1977; Ichthyophidae Taylor, 1969; Scolecomorphidae Taylor, 1969; Chikilidae Kamei *et al.*, 2012; Herpelidae Laurent, 1984; Caeciliidae Rafinesque, 1814; Typhlonectidae Taylor, 1968; Indotyphlidae Lescure *et al.*, 1986; Siphonopidae Bonaparte, 1850 and Dermophiidae Taylor, 1969.

With the discovery and subsequent description of Rhinatrematidae, the caecilian diversity was subdivided between this family and the suprafamiliar taxon Neocaecilia, which comprised all the other species of modern caecilians (Wilkinson & Nussbaum, 2006). The first proposed name for the clade comprising all modern caecilians except rhinatrematids was Stegokrotaphia (Canatella & Hillis, 1993). However, as pointed by Wilkinson & Nussbaum (2006), such terminology is quite problematic, as the group encompasses a great variety of zygokrotaphic species of typhlonectids, caeciliids and scolecomorphids.

Therefore, the terminology Neocaecilia, being anatomically neutral, was proposed to designate this taxon. Typically found in the Neotropics, rhinatrematids encompass two genera (*Rhinatrema* and *Epicrionops*), and its monophyly is well-supported by molecular and morphological data (Nussbaum, 1977; Wilkinson, 1992; San Mauro *et al.*, 2014; Maciel *et al.*, 2018). Unique features include the presence of a squamosal notch that articulates with an os basale process, and an opened skull roof in which the paired *m. adductores mandibulae externi* reach the dorsal skull midline (Nussbaum, 1977; Wilkinson & Nussbaum, 2006).

Neocaecilia was recovered as a natural group in most phylogenetic analyses, regardless of the data source and always with a high support values (e.g. Wilkinson, 1997; Pyron & Wiens, 2011; Maddin *et al.*, 2012b; Maciel *et al.*, 2018). Some of the synapomorphies include a long and curved retroarticular process, sides of the paraesphenoid converging laterally, absence of contact between the quadrate and the maxillopalatine, jaw closing muscles, paired *m. adductores mandibulae externi* not meeting mid-dorsally in skull, narrow and elongated ventricle, bipartite *sinus venosus*, among others (Wilkinson & Nussbaum, 2006).

The Ichthyophiidae encompasses three genera (*Ichthyophis*, *Caudacaecilia*, and *Uraeotyphlus*) distributed in South and Southeast Asia, characterized by a partial external division of the atrium and a large anterior pericardial space (Nussbaum, 1979; Wilkinson & Nussbaum, 1996). Although their monophyly is well-established, relationships

between these genera are still not completely clear, since *Ichthyophis* and *Caudacaecilia* differ only in a character known to be homoplastic among caecilians, i.e., the presence or not of an interior dental arch in the mandible in adults (Nussbaum, 1979). In addition, in some analyses *Ichthyophis* was considered paraphyletic in respect to *Caudacaecilia* (e. g. Roelants *et al.*, 2007; Maddin *et al.*, 2012b).

Initially, a subfamily of the Ichthyophiidae (Nussbaum, 1979), the Uraeotyphlinae was posteriorly raised to the familial level (Duellman & Trueb, 1986). However, subsequent morphological and molecular phylogenetic analyses did not corroborate this proposal (e.g. Gower *et al.*, 2002; Roelants *et al.*, 2007), showing that the recognition of Uraeotyphlidae would entail the paraphyly of *Ichthyophis*. Therefore, following the solution proposed by Frost *et al.* (2006), Uraeotyphlidae is considered a junior synonym of Ichthyophiidae, whereas the problem of paraphyly remains at the generic level.

The Teresomata, informally called advanced caecilians, includes the families Scolecomorphidae, Herpelidae, Chikilidae, Typhlonectidae, Caeciliidae, Indothyphlidae, Siphonopidae and Dermophiidae (Nussbaum, 1991; San Mauro *et al.*, 2004). Although this group has been recovered with strong support values in all molecular and morphological phylogenetic analyses, only two synapomorphies are known for it, the absence of internal flexures in m. *rectus lateralis* and the lack of a true tail (Nussbaum & Naylor 1982; Wilkinson & Nussbaum, 2006).

The Scolecomorphidae includes species from East and West Africa allocated in the genera *Crotaphatrema* and *Scolecomorphus* (Taylor, 1969; O'Reilly *et al.*, 1996). Its monophyly has been recovered in most morphological (e.g. Wilkinson, 1997; Maddin *et al.*, 2012b) and molecular (e.g. Loader *et al.*, 2007; Doherty-Bone *et al.*, 2011; San Mauro *et al.*, 2014) phylogenetic analyses. The genera share several uniquely derived features, such as the absence of stapes, *foramina ovalis* in adults, and internal processes in the lower jaws, as well as mobile eyes located at the base of the tentacles (Nussbaum, 1985).

Some older phylogenetic works, based on molecular (Frost *et al.*, 2006; Loader *et al.*, 2007) and low-resolution neuroanatomical (Wilkinson, 1997) data, recovered an alternative position for scolecomorphids within “Caeciliidae”, leading to paraphyly of the latter. However, most recent analyses have not recovered this topology, corroborating the hypothesis that Scolecomorphidae forms a monophyletic clade distinct from “Caeciliidae”, no longer considering it as a junior synonym (e.g. Wilkinson *et al.*, 2011).

The African Herpelidae comprises two genera (*Herpele* and *Boulengerula*). In many phylogenetic analyses these two genera were retrieved nested inside “Caeciliidae”, among other groups of “advanced caecilians” (e.g. Frost *et al.*, 2006). However, in current classifications, the group has appeared as a separate clade due to modifications that restricted the definitions and content of Caeciliidae. They differ from chikilids and the other caecilians by exhibiting multiple anomalous antotic foramina on each side of the skull and by lacking separated prefrontals (Kamei *et al.*, 2012).

Typically found in the northeastern region of the Indian subcontinent, the Chikilidae contains only one known genus, *Chikila*, and was the last caecilian family to be formally recognized, although the type species *C. fulleri* (Alcock, 1904) has been described more than 100 years ago under the name *Herpele fulleri* (Kamei *et al.*, 2013). Despite the superficial similarities, they are distinguished from herpelids by the presence of an undivided antotic foramen on each side of the skull and frontals that not reaching the skull roof posterior to the sphenethmoid, among other features (Kamei *et al.*, 2012).

As Caeciliidae traditionally received all the described species of caecilians, even with the advance in the understanding of phylogenetic relationships within Gymnophiona, this group continued to accommodate all species that have not yet been assigned to other families, being recovered as a paraphyletic taxon in multiple analyses based on morphology and molecular data (Wilkinson & Nussbaum, 2006). Several strategies have been proposed to address the paraphyly of Caeciliidae, including condering Typhlonectidae and Scolecomorphidae (e.g. Hedges *et al.*, 1993; Frost *et al.*, 2006) as junior synonyms of Caeciliidae.

In order to solve the problem of Caeciliidae paraphyly, the clade was restricted to only two genera, *Caecilia* and *Oscacaecilia*, following the solution proposed by Wilkinson *et al.* (2011). According this interpretation, Caeciliidae is the sister group of Typhlonectidae, forming an unnamed monophyletic group characterized by the presence of a nasopremaxilla and moncuspid teeth. When compared to the time of divergence from other caecilian lineages, estimates suggest that the separation between these two families is one of the most recent, dating back to the Upper Cretaceous (Zhang & Wake, 2009; Maciel *et al.*, 2016).

The Caeciliidae (*sensu* Wilkinson *et al.*, 2011) are typical of Central and South America. Although *Caecilia* and *Oscacaecilia* are morphologically very similar, only a few

unambiguous morphological synapomorphies support the monophyly of the family that receives strong molecular support (Wilkinson, 1997; Maddin *et al.*, 2012b; San Mauro *et al.*, 2014). Commonly derived characteristics include eyes covered or surrounded by the maxillopalatine, inner mandibular tooth row in the lower jaw and unperforated stapes (Wilkinson *et al.*, 2011).

The Typhlonectidae, which includes South American species that are well-adapted to aquatic and semi-aquatic environments (Nussbaum & Wilkinson, 1989), has a total of five genera: *Chthonerpeton*, *Nectocaecilia*, *Atretochoana*, *Potomotyphlus*, and *Typhlonectes* (Wilkinson & Nussbaum, 1997). Its monophyly is well established and supported by molecular and morphological data (Wilkinson, 1997; Wilkinson & Nussbaum, 1999; Maciel *et al.*, 2016). Uniquely derived characters include fused sac-shaped fetal gills, small tentacle openings, and relatively dorsally oriented occipital condyles (e.g. Wilkinson & Nussbaum, 1999; 2006).

Recovered in the vast majority of phylogenetic analyses based on molecular data (e.g. Zhang & Wake, 2009; San Mauro *et al.*, 2014), the Indotyphlidae includes seven genera (*Gegeneophis*, *Grandisonia*, *Hypogeophis*, *Idiocranium*, *Indotyphlus*, *Praslinia* and *Sylvacaecilia*), found in the island of Seychelles and India, with no unambiguous synapomorphy known so far (Wilkinson *et al.*, 2011; Gower *et al.*, 2011). However, its diagnosis can be made by the presence of a set of characters, being the only caecilians to simultaneously exhibit unperforated stapes, some bicuspid teeth, eyes located between the squamosal and maxillopalatine border, inner tooth row in lower jaw and viviparity (without secondary scales or rings) or oviparity (Wilkinson *et al.*, 2011).

Five genera constitute the family Siphonopidae of South American caecilians (*Brasilotyphlus*, *Luetkenotyphlus*, *Microcaecilia*, *Mimosiphonops*, and *Siphonops*). These taxa are morphologically very similar to each other, and traditionally phylogenetic analyses include only few representatives of this clade (e.g. San Mauro *et al.*, 2004; Roelants *et al.*, 2007; Zhang & Wake, 2009; but see Correia *et al.*, 2018 for a more extensive analysis). Siphonopids are the only oviparous caecilians with unperforated stapes and without an inner dental row in lower jaw (Wilkinson *et al.*, 2011).

The Dermophiidae, which comprises four genera of caecilians from Africa, Central and South America (*Dermophis*, *Geotrypetes*, *Gymnopsis*, *Schistometopum*), has been recovered with strong support values in most recent phylogenetic analyses based on

molecular data (e.g. Loader *et al.*, 2007; Zhang & Wake, 2009; San Mauro *et al.*, 2014). It includes species characterized by their viviparity and the presence of annular scales and secondary annuli (Wilkinson *et al.*, 2011). Initially defined by Taylor as a subfamily (1969), the Dermophiidae grouped a paraphyletic assemblage of “caeciliids.” Posteriorly, Laurent (1984) elevated the same clade to the family category. Therefore, although the current content of Dermophiidae differs substantially from that considered by these authors, the name remains as the oldest available for this taxon (Wilkinson *et al.*, 2011).

In conclusion, despite important advances made in the last decades, some problems persist in caecilian systematics. Although the currently most accepted proposal has managed to eliminate the paraphyly of Caeciliidae (in relation to the other “advanced caecilians”) and Ichthyophiidae (in relation to Uraeotyphlidae) at the familial level, issues of paraphyly persist at the generic level, being one of the future challenges in the area (Wilkinson *et al.*, 2011). In addition, the clade formed by Indotyphlidae, Siphonopidae and Dermophiidae still needs to be resolved, as unambiguous derived characteristics are lacking for it.

1.4. Biogeography



Figure 8: Distribution of modern caecilians. Modified from Cogger & Zweifel (1998) and Loader *et al.* (2007).

Gymnophiona is known by its pantropical distribution (Figure 8), focused on areas of Central and South America, East and West Africa, India and other parts of South and

Southeast Asia (Zhang & Wake, 2009). Based on this distribution, the first biogeographic proposals for the group were generally based on the hypothesis of a Gondwanan origin and subsequent diversification associated with the fragmentation of these landmasses, in addition to occasional dispersions to portions of Laurasia (e.g. Duellman & Trueb, 1986).

However, the limited fossil record of caecilians shows that the oldest known occurrences for the group come from deposits located in northern continents (e.g. Jenkins *et al.*, 2007). Additionally, the separation of several Gymnophionomorpha lineages does not seem to be directly linked to vicariance events, and therefore the typical Gondwanan signature is absent in such cases. According to the most recent biogeographical hypotheses, the evolutionary history of caecilians is characterized by the occurrence of geographically restricted lineages, with low rates of speciation and dispersion, and the landmasses breakup did not cause these patterns, only reinforced the already present high spatial partition (Kamei *et al.*, 2012).

The divergence between the lineages of Rhinatrematidae, Scolecomorphiidae and the clade Caeciliidae plus Typhlonectidae also seems to be independent of vicariance events linked to the movement of tectonic plates (Duellman & Trueb, 1994; Gower & Wilkinson, 2009). However, unlike the groups mentioned above, the endemic occurrence of the Chikilidae in India is directly related to the geological events associated with the movement of the Indian plate, since phylogenetic analyses indicate that this taxon is closely related to herpelids, a family of African caecilians. Thus, the chikilids were already present in Greater India (supercontinent formed by Madagascar, India and Seychelles) during its isolation and subsequent movement towards the north (Kamei *et al.*, 2012).

Regarding Ichthyophiidae species, different hypotheses were proposed to explain its distribution in India and South East Asia. Traditionally, the presence of this group in South and Southeast Asia was explained by the vicariance followed by dispersion, from the collision of Indian plate during the Cretaceous (Duellman & Trueb, 1986; Gower *et al.*, 2002). In an alternative and now considered a less robust hypotheses, ichthyophiids were isolated in Laurasia at the time of its separation from Gondwana or reached such areas from nearby Gondwanan portions during Jurassic or Early Cretaceous, and then later, also through a dispersion event, they occupied the portions of India in which they are found today (Hedges *et al.*, 1993).

Recently, Maciel (2016, chapter 5) proposed correlations between the evolution of typhlonectids and changes in the South America landscape. According to its results, this group was already widespread in the northern areas of South America during the Late Cretaceous. *Chthonerpeton* dispersed towards Southeast and Northeast basins and was extinct in almost all northern basins, whereas part of the divergence of some the fully aquatic taxa (*Typhlonectes*, *Potomotyphlus*, and *Atretochoana*) could be related to the division of eastward and westward flowing rivers by the Purus Arch.

Although biogeographic knowledge is not available for all caecilian taxa, the increase in the availability of caecilian molecular data and the collection of new specimens with an improvement in the resolution of their localities of origin, along with the description of new fossils will certainly contribute to change this scenario.

1.5. Natural History and Ecology

Among all living tetrapod groups, caecilians remain as the least known, although efforts over the years of research promoted a considerable advance in the understanding of these animals (Zhang & Wake, 2009). Numerous factors contribute to this scenario, with emphasis on the difficulties in observing and collecting specimens, as most species exhibit fossorial habits and live in tropical forests areas that are difficult to access (Gower & Wilkinson, 2005). Not surprisingly, a considerable portion of the species is known from few specimens, whose type locality is not so precise (e.g. Nussbaum & Wilkinson, 1995; Maciel & Hoogmoed, 2011).

Despite all these limitations, important advances have occurred in recent years, especially after the publications of Taylor (1968; 1969). Even in the absence of direct observations in the natural environment, many aspects related to the biology of caecilians can be accessed indirectly, from inferences based on its morphology (Jared *et al.*, 1999). For example, the presence of fins and the reduction and/or absence of lungs in certain species can be used to infer the occurrence of aquatic habits, even though no direct observation of these individuals in nature has occurred (e.g. Wilkinson & Nussbaum, 1999).

Despite the significant increase in knowledge about caecilian ethology based on studies with captivity animals (e.g. Exbrayat & Delsol, 1985; Sutharam *et al.*, 1990), problems inherent to the observation of behaviors in the natural environment continue to

hinder advances in the area (Savage & Wake, 1972). In these observations, the ability to dig varies between families, and individuals seem to spend most of their time moveless and/or hiding (although this may be related to a limited amount of observations in nature, as shown by Jared *et al.*, 1999), preferring to use pre-existing tunnels rather than dig new ones. Therefore, even considering that the behavior of excavating the soil requires high metabolic capacities, as they lived in a habitat that are low in oxygen, it is expected that caecilians present low levels of activity and behaviors that reduce their energy costs (Ducey *et al.*, 1993).

Depending on the lifestyle and substrate characteristics, the form of locomotion of caecilians can vary (Jared *et al.*, 1999; Herrel & Measey, 2010). The most typical movements performed by these animals include lateral body undulations (which predominate in species of aquatic habits), internal concertina (Summers & O'Reilly, 1997) and wormlike movements (used inside pre-existing tunnels or while the animal is digging in compact soil) (Nussbaum & Naylor, 1982). The typhlonectid *Chthonerpeton indistinctum*, known by its semi-aquatic habits, is able to swim and move easily in muddy soils (Gudynas & Williams, 1986; Gudynas *et al.*, 1988).

In nature, the caecilian diet varies according to the species and its ontogenetic stage. Larvae usually feed on arthropods and other invertebrates, while adult individuals feed on small molluscs, arthropods and annelids or, in the case of *Typhlonectes compressicauda*, fish carcasses and aquatic arthropods (O'Reilly, 2000). The consumption of vegetal matter has been reported for different species, including plant remains, some of them already in a decomposition stage, soil particles and fibers (e.g. Hebrard *et al.*, 1992). In captivity, specimens are usually fed with earthworms, frozen fish, minced meat or mice (Jared *et al.*, 1999).

Based on observations, mainly from captive individuals, caecilians are able to hunt actively their prey, developing slightly different methods for obtaining their food. Some species attack with bite and swallow their prey directly, while others try to take them into tunnels, where they are finally swallowed (O'Reilly, 2000). Additional strategies include surrounding the prey with its own body, thus preventing a possible escape, or performing quick rotational moves while it is taken underground (Bennett & Wake, 1974).

Recently, an oral venom system was discovered and described for caecilians. According to Mailho-Fontana *et al.* (2020), caecilians have tooth-related glands in both jaws, with a similar origin to reptile venom glands, capable of secreting enzymes usually present in venoms. These glands are already present in basal taxa, such as *Rhinatrema*, showing that the capacity to produce and inject oral toxins appeared early among caecilian lineages, probably independently from other tetrapods.

1.6. Gymnophionan Physiology and Reproduction

The cardiovascular system of caecilians exhibits significant differences when compared to the other amphibian groups. The decrease in the size of red blood cells, an adaptation to environments with low oxygen availability found in some anurans (Czopek, 1983), does not occur in Gymnophiona (Sano-Martins *et al.*, 1990). On the other hand, the hemoglobin concentration in some species was higher when compared to anurans and urodels (Toews & Macintyre, 1978). Apparently, a functional bone marrow is absent in caecilians (Paillot *et al.*, 1997).

Caecilians can show different strategies to execute their gas exchanges, a reflex of a great ecological diversity. To do this, they can use lungs, gills or integument, depending on the species, habitat and the ontogenetic stage in which they are (Toews & Macintyre, 1978; Nussbaum & Wilkinson, 1995). In gymnophionans, only one of the lungs is functional, and the undeveloped side is related to the phylogenetic relationship of the species (Jared *et al.*, 1999). In some species of Typhlonectidae, both lungs have been completely lost (e.g. Maciel *et al.*, 2016). Unlike the pattern found in other groups of amphibians, the exhalation of caecilians occurs passively (Bennett & Wake, 1974).

As in other lissamphibians, caecilian skin is permeable, making them susceptible to water and electrolytes loss, although adaptations such as life in fossorial or aquatic environments prevent dehydration (Duellman & Trueb, 1994). Processes related to the excretion of nitrogenous metabolic wastes are still poorly understood, but it is known that they release urea and ammonia through the kidneys and mainly by the skin. In aquatic species, with a tendency to lose water and electrolytes due to subcutaneous diffusion or by urine, the bladder usually performs the osmotic control (Stiffler & Manokham, 1994).

The caecilian sensory system exhibits several adaptations for survival in the fossorial environment. Most of the species are virtually blind when adults, having only

the capacity to distinguish light and dark environments (Wake, 1985). As they do not have a tympanic membrane, its hearing is poorly developed, but they are capable to produce sounds and communicate through them (Fritsch & Wake, 1988). In the aquatic larval stage, the lateral line is present, capturing mechanic and electrical stimuli from the surrounding environment (e.g. Taylor, 1970; Hetherington & Wake, 1979; Wilkinson, 1992; O'Reilly, 2000).

The senses related to chemical reception are the most developed in caecilians. The olfactory brain lobes, which are larger when compared to other amphibians, are the main indicatives of a well-developed smell sense. The most characteristic sensory organs of caecilians, the tentacles, positioned laterally in the skull and capable of retracting or protruding, have chemoreceptive and tactile functions (Billo & Wake, 1987). Therefore, its presence was certainly one of the factors that contributed to the conquest of the fossorial environment by caecilians (Wake, 1993).

Although several aspects of the caecilian reproduction remain virtually unknown, such as the attraction between individuals and courtship behaviors, some reproduction strategies have already been described in the literature (Wake, 2006). Unlike other amphibian groups, most gymnophionans are viviparous (Wake, 1977). Since fertilization is internal, males have an eversible copulatory organ, the phallus, capable of storing liquids for the sperm transport (Exbrayat & Estabel, 2006). The ontogenetic development can be direct or indirect, and the period of larval phase, which can be aquatic in some groups, varies according to the taxon (Wake, 2006).

The viviparous reproduction requires a series of adaptations, which include the modification of the posterior portion of the oviduct, forming a "uterus", capable of receiving and feeding the embryos through nutrient-rich secretions after the end of yolk (Exbrayat & Estabel, 2006). The development of special teeth in juveniles is also an adaptation to viviparity, as fetal teeth are used to pull parts of the uterus walls, absorbing them along with nutritive secretions, which also seems to stimulate the production of more secretion (Kupfer *et al.*, 2006).

2. Objectives

The main objective of the present study is to describe the morphology and analyze the phylogenetic affinities of an articulated skeleton of caecilian from the Oligocene of Brazil. This is the first South American specimen of caecilian known so far to retain a partially preserved skull and articulated axial skeleton. The specimen belongs to the collection of the Museu de Ciências da Terra, where it is registered under the accession number DGM 1462-R.

Further objectives of this study are as follow:

- Review and discuss the caecilian fossil record, including the crown-group (Gymnophiona) and the stem lineages (Gymnophionomorpha);
- Describe in details the anatomy of the specimen DGM-1462-R and compare its features with other caecilians;
- Include it in a phylogenetic analysis encompassing taxa of all known caecilian extant families and test its positioning within Gymnophiona.

3. Geological Background

The specimen DGM 1462-R was found in rocks belonging to the Tremembé Formation, which is Oligocene in age and known by its rich fossiliferous content. Detailing the origins and development of these and other adjacent deposits is crucial for a more complete understanding of the fossils found there, including aspects of their age, ecology, taphonomy, and biogeography.

3.1. The Cenozoic Rifts System of Southeast Brazil

With approximately 900 km of length and located between the states of Paraná and Rio de Janeiro, the Cenozoic Rifts System of Southeast Brazil (CRSSB) comprises a series of elongated and narrow depressions dated from Paleocene (Zalán & Oliveira, 2005). The CRSSB (Figure 9) was developed upon gneisses, migmatites and other metamorphic rocks of the Cinturão de Dobramentos Ribeira (Hasui *et al.*, 1975), as well as other packages of neoproterozoic intrusive granite rocks (Janasi & Ulbrich, 1991), in an event linked to the opening of the South Atlantic Ocean (Saenz *et al.*, 2003).

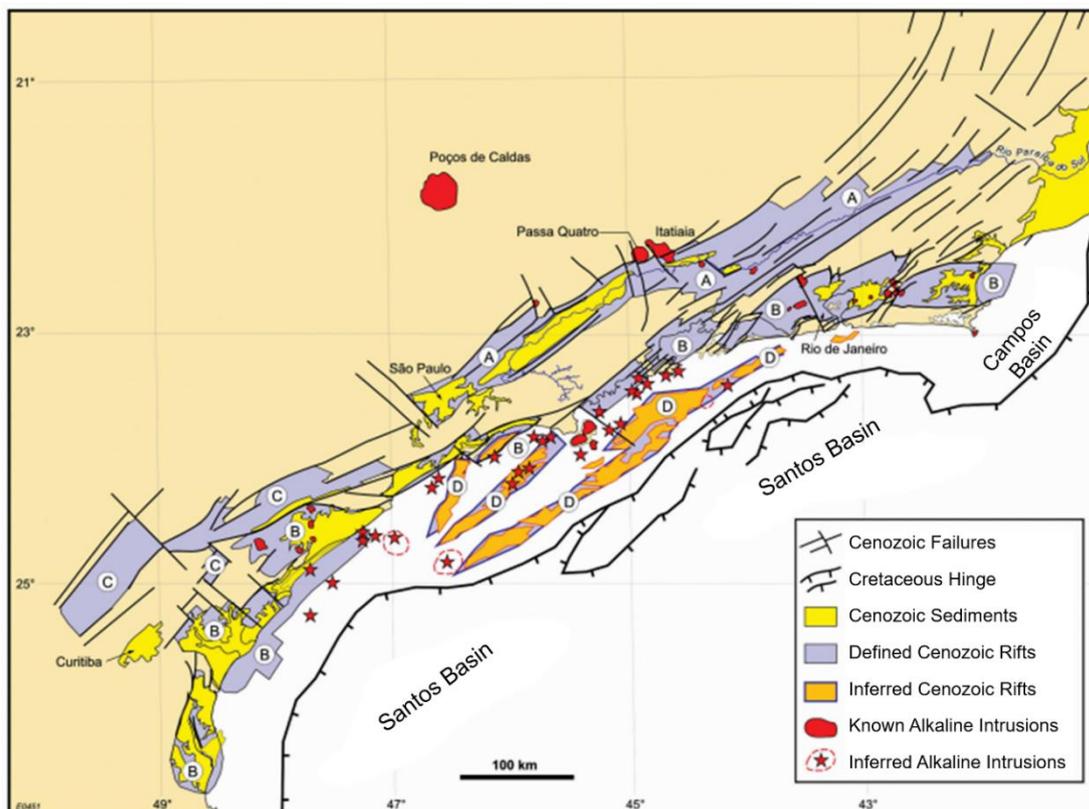


Figure 9: Map with the distribution of the four rifts that form the Cenozoic Rifts System of Southeast Brazil. A) Paraíba Do Sul. B) Litorâneo. C) Ribeira. D) Marítimo. Modified from Zalán & Oliveira (2005).

Altogether, the CRSSB encompasses important Cenozoic sedimentary basins, including five main ones (Curitiba, São Paulo, Taubaté, Resende and Volta Redonda) and others with more restricted distribution areas (São José de Itaboraí and Barra de São João) (Riccomini, 1989). Despite the different models agree that the formation of such basins is closely linked to the tectonic and morphogenetic events that led to the origin of the Serra da Mantiqueira and Serra do Mar, they still disagree about the mechanisms that generated such events (Freitas, 2007).

The CRSSB can be divided into three main segments along its length. A western one, which comprises the Curitiba Basin, the grabens of Guaraqueçaba, Cananeia and Sete Barras and the Alexandra and Piraquera-Açu Formations. An eastern one, which includes the Basins of Macacu, São José de Itaboraí and the Barra de São João graben, and a central one, which stands out for its wide distribution area, encompassing the São Paulo, Taubaté, Resende and Volta Redonda Basins, along with other deposits in the regions of Bonfim and Cafundó (Riccomini *et al.*, 1996; Freitas, 2007).

3.2. CRSSB Research History

The set of Cenozoic grabens located in southeastern Brazil received attention from several researchers from different Geoscience areas. The first proposal for the recognition of the link between the origins of the sedimentary basins established in depressions of tectonic origin with the adjacent mountainous regions, whose uplift is related to faults, among which the Serra do Mar stands out, was proposed by Almeida (1976). When relating such features, this author coined the term *Sistema de Riftes da Serra do Mar*.

Posteriorly, Melo *et al.* (1985) proposed the term Continental Tectonic Basin System of Southeast Brazil, recognizing similarities in the characteristics and chronology of events related to the origin of the four main basins in the region (São Paulo, Taubaté, Resende and Volta Redonda), in which the structural framework was interpreted as a set of half-grabens placed on tectonic blocks whose tilting follows NW direction. Such factors allowed the authors to consider that the evolution of these basins took place in a homologous way, that is, with all of them subject to the same processes of regional distension.

When coining the term "Continental Rift of Southeast Brazil" (CRSB), Riccomini (1989) emphasizes its continuous characteristic at the time of its origin (hence the use of

rift in singular), its continental condition (referring to an emerged area, which differentiates from the Santos Basin, located in the adjacent oceanic portion) and a greater range (since *Serra do Mar* is only one of the relief features related to the Rift).

The most recent terminology, Cenozoic Rifts System of Southeast Brazil (CRSSB), was coined by Zalán & Oliveira (2005) and seeks to concatenate the various related geological events. Among them, stands out a westward landslide of the South American Plate during Late Cretaceous over a thermal anomaly, which caused the basement uplift, the intrusion of alkaline stocks and the formation of a large plateau, originated from the Japi Surface flattening, the individualization of the blocks caused by gravitational instability and their differential vertical movement, in addition to the effusion of alkaline lavas during the Paleogene. The products generated through the weathering of all these elements were deposited in two subsidiary basins located beside.

Considering that the variance between mountains and depressions and/or plains is related to a succession of staggered and asymmetrical horsts and grabens, with failed and flexural edges, accommodation areas and transfer failures that segment them into sub-grabens, the interpretation proposed by Riccomini (1989) of a single and continuous rift was not corroborated by the hypothesis of Zalán & Oliveira (2005). In this way, the numerous and different rifts are interpreted as depressed tectonic valley corridors along normal planar and rotational faults, and the terms graben and sub-graben were used to designate smaller tectonic compartments within the larger rifts, while the Basins can be understood as eventual accumulations of sediments that occur inside the grabens.

3.3. The Taubaté Basin

The Taubaté Basin (Figure 10) is considered of Intracontinental Rift type, oriented towards ENE, asymmetrical, whose interior is formed by areas with depressions, which correspond to the sub-basins of Parateí, Jacareí, Eugênio de Melo, Tremembé, Lorena and Cruzeiro, separated from each other by higher regions, including the tips of Rio Putins, Caçapava, Aparecida and Cachoeira Paulista (De Carvalho *et al.*, 2011). Its longest axis is about 170 km, and the average width is 20 km. Although only the upper 200 m are well known (Saad, 1991), the average sedimentary thickness is approximately 500 m, although in some places it can reach around 800-900 m (Fernandes, 1993).

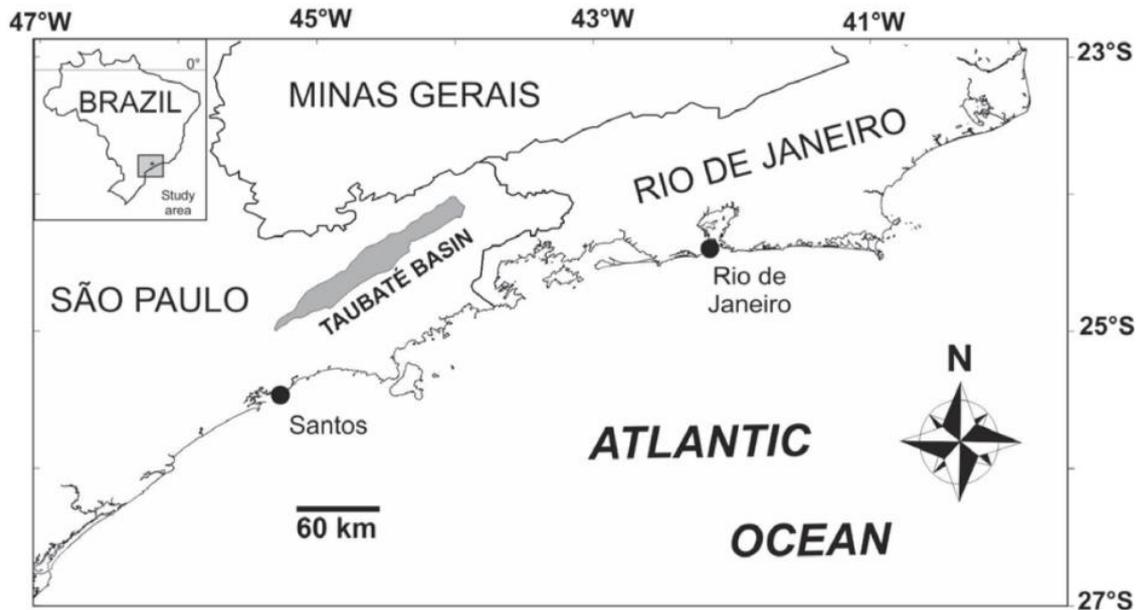


Figure 10: Map of Taubaté Basin. Modified from Bergue *et al.* (2015).

According to some estimates, the sediments that filled the depression in the Taubaté Basin were deposited between 34 and 25 million years ago, during the Oligocene and in a syntectonic way (Lima *et al.*, 1985; Torres-Ribeiro, 2004). Sediments are typically continental, with a thicker granulometry at the failed edges of the basin, while sandstone and mudstone deposits are predominant at the central portions, including layers of pyrobituminous shales, indicative of a fluvio-lacustrine depositional environment.

It was only after the highly detailed mapping in the pioneering work of Derby (1895), that the Taubaté Basin became well understood. Later, Washburne (1930) and Moraes-Rego (1933) recognized the existence of differences between the sedimentary packages that made up the basin. This hypothesis was corroborated in several other subsequent works (e.g. Suguio, 1969; Carneiro *et al.*, 1976), in which lithological differences between the layers were identified and described.

Currently, three lithostratigraphic units are recognized for the Taubaté Basin: Resende Formation, Tremembé Formation and Pindamonhangaba Formation (Vidal *et al.*, 2004). The first corresponds to a system of proximal alluvial fans, associated with braided rivers plain located in the most lateral portion of the Basin (Ramos *et al.*, 2006). The second comprises a playa-lake system, composed of fine sediments arranged in pyrobituminous shales, interspersed with greenish clays beds (Riccomini, 1996). The latter has sediments deposited in the context of a meandering river system (Riccomini *et al.*, 1991b).

3.4. Resende Formation

The most representative lithostratigraphic unit in terms of area and volume in the Resende and Volta Redonda basins, this formation also develops in other basins in the central segment of the CRSSB, including in Taubaté Basin. Initially defined by Amador (1975), which characterized it by the presence of greenish sandstones of fine to coarse granulometry, arranged as massive structures or in channeled cross-stratification, in addition to eventual conglomerate layers, siltstones and mudstones. Its sedimentation occurred during the rift phase, in which depositional systems of alluvial fans are associated with braided river systems and flood plains (Ramos *et al.*, 2006).

The main lithofacies associated with the Resende Formation, according to Garcindo (2009), include polymeric conglomerates supported by the matrix, related to a depositional environment of proximal alluvial fans, along with arkose arranged in cross-stratification and mudstones with occasional conglomerates, representing a depositional system of intermediary alluvial fans or braided river channels, in addition to massive sandstones and claystones that rarely show bioturbation signals. These latter deposits are usually related to flood plains (Riccomini *et al.*, 1991a).

Based on the redefinition of the Itatiaia Formation, Ramos (2003) individualized two members in the Resende Formation. The Itatiaia Member comprises deposits rich in alkaline rock clasts (related to alluvial and fluvial fan deposits) and the Acácias Member, located at the top of Resende Formation, characterized by the presence of thick levels of massive pelites, in addition to ascending cyclical layers of conglomerates-sandstone-pelites up to 4m thick (associated with a braided river system).

Pedogenetic elements were observed and associated with flood plains, including pelite beds (Ramos, 2003) and caliches (Sanson, 2006). Garcindo (2009) recognized two pedofacies, including levels with a high degree of bioturbation and manganese rhizoconcretions. Although paleofauna is still unknown for this unit, palinomorph records are frequent, providing data for paleoclimate interpretations, which indicate a hot and wet depositional system (Lima & Melo, 1994). The fossiliferous content of the Resende Formation is extremely limited, being restricted to ichnofossils and fossil wood (Scheel-Ybert, 2007).

3.5. Tremembé Formation

According to the current conception, the Tremembé Formation corresponds to a lacustrine system, deposited in a semi-arid climate, located in the central portion of the Taubaté Basin, dating back to the Oligocene, interdigitated laterally and vertically with Eocene deposits associated with the Resende Formation and covered by the Pindamonhangaba Formation (Freitas, 2007). Analyses obtained from survey data and outcrop observations allow the recognition of the main lithofacies associated with this formation, including marl and shale rhythmites, solid greenish mudstones, dolomite and sandstone (Riccomini, 1989; Riccomini *et al.*, 1996).

The rhythmites are formed from the alternation of sheets or layers of shales and marls with centimetric thickness. The shales have a color ranging from brown to gray, sometimes pyrobituminous and frequently fossiliferous (Suguio, 1969). The marls are also rich in fossils, especially ostracodes, and can gradually scale to limestone. Solid greenish mudstones facies, with a numerous fossil record, exhibit metric thickness and eventually contraction cracks and calcium rich concretions.

The variation in rock types found in the Tremembé Formation can be attributed to variations in salinity, evaporation rates and the thickness of the water layer (Riccomini, 1989; Sant'anna, 1999). Thus, dolomites represent moments of predominance of high rates of evaporation and salinity (Sant'anna, 1999). The greenish mudstones were deposited in periods of shallower water depth, while layers of shales are related to lacustrine sedimentation in times of greater depth. On the edges of the Taubaté Basin, fine to medium sandstones are also present, arranged in thick cross stratifications, deposited in delta fans adjacent to the lake north edge (Riccomini, 1989).

The cyclic deposition of papyraceous shales, recognized by Riccomini *et al.* (1996), is evidenced by the alternation between the narrow light layers (interpreted as winter deposits) and dark (representative of summer deposits). The regular spacing between layers is possibly related to the Milankovitch's astronomical cycles. Because they exhibit high levels of kerogen, these packages are interpreted as pyrobituminous shales. Estimates suggest that the deposition of the Tremembé Formation was temporally restricted, occupying an interval of only 650 thousand years, a small value when compared to the Oligocene total range, estimated at about 13 million years (Riccomini *et al.*, 1993).

As mentioned above, the Tremembé Formation represents a predominantly lacustrine depositional system (Riccomini, 1989). Such environments are described as water bodies not directly connected to the oceans, formed from a pre-existing depression on the surface, in a region whose water balance is favorable (Wetzel, 2001). According to Torres-Ribeiro (2004), the water depth of the Tremembé lake was variable, with moments of greater thickness (10 m) alternating with shallower periods (5 m), also characterized by an increase in salinity, with emphasis on the increase in Calcium Carbonate concentration.

3.6. Pindamonhangaba Formation

Initially, most part of sedimentary packages that are currently assigned to the Pindamonhangaba Formation were determined as belonging to the Caçapava Formation (Carneiro *et al.*, 1976), a unit that also included deposits later attributed to the Resende Formation (Riccomini, 1989). The change in terminology is justified, since the Caçapava Formation included very different deposits in its lithology, separated by a regional discordance. Additionally, the terminology Granito Caçapava (Teixeira, 1937) was coined first, and therefore there is a priority in its usage.

As initially defined by Riccomini *et al.* (1991b), the Pindamonhangaba Formation, with Neocenoic age, comprises well-developed deposits along the Taubaté Basin central area, whose maximum estimated thickness is approximately 30 m. It is also characterized by the presence of flat surfaces at its top, a feature originated from the lateral persistence and planarity of the deposits that constitute it, observed in the various plateaus in the regions of Caçapava, Taubaté and Pindamonhangaba, remnants of this surface and today undergoing carving processes.

In its packages, seven main lithofacies can be recognized, including basal facies of pebbles dispersed in thick sandstones; facies of coarse sandstones with a matrix rich in clay and eventual conglomerates, arranged in tabular cross stratification; facies of fine to medium sandstones arranged in grooved decametric trough cross-beds; facies of solid silicate, stratified or laminated, with metric thickness; facies of conglomeratic sandstones dispersed in siltstone and mudstone matrix; facies of medium to coarse sandstones, grading to siltstones and mudstones, arranged in plane-parallel stratifications and facies of mudstones rich in sand.

This set of facies allows to associate the origin of the Pindamonhangaba Formation deposits to a meandering river system (Riccomini *et al.*, 1991b). The fossiliferous content of this unit includes caracid fish (Vicalvi, 1982) and several plant records, including trunks and leaf impressions, from the Rubiaceae, Myrtaceae, Melastomataceae, Styracaceae, Equisetaceae, Sapindaceae, Sapotaceae, Anacardiaceae and Symplocaceae families (Tufano, 2009). The occurrence of these plants, along with the abundance of detritic kaolinite indicate more wet climatic conditions (Riccomini, 1989).

3.7. The Fossil Record of the Tremembé Formation

The Tremembé Formation fossiliferous content is extremely numerous and diverse, encompassing records of ichnofossils, plants (including palynomorphs, leaf impressions and trunk fragments), invertebrates and vertebrates (Torres-Ribeiro & Borghi, 2007). The main places for fossil collection comprise outcrops exploited commercially, mostly focused in montmorillonite clay, with emphasis on an area belonging to Sociedade Extrativa Santa Fé Ltda., known as Fazenda Santa Fé.

Considering the occurrence of fossil vertebrates, the fish (Perciformes, Characiformes and Siluriformes) are the most abundant, coming mainly from pyrobetuminous shale levels, where a small Chiroptera was also found. The remaining fossil groups, however, are predominantly found in montmorillonite clay levels, and include amphibians (Anura), turtles (Chelidae), snakes, alligators (Alligatoridae), birds (Galliformes, Anseriformes, Gruiformes, Falconiformes and Teratornithidae), and mammals (Metatheria, Cingulata, Rodentia, Litopterna, Astrapotherata, Notoungulata and Pyrotheria; see Ribeiro, 2010).

The invertebrate record is equally rich, encompassing indeterminate porifers, mollusks (Gastropoda), crustaceans (Decapoda, Ostracoda and Isopoda) and insects (Hemiptera, Lepidoptera, Diptera, Homoptera, Trichoptera Hymenoptera, Coleoptera and Orthoptera; see Ribeiro, 2010). Ichnofossils are also present, mainly with traces attributed to annelids and numerous coprolites (Castro *et al.*, 1988; Bergqvist & Ribeiro, 1998).

4. The Fossil Record of Gymnophionomorpha and its use to calibrate molecular timetrees*

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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 (e. g. Schoch & Millner, 2004; Marjanović & Laurin, 2014, 2019). This scarcity is particularly pronounced for caecilians. For many years, only one caecilian was known in the fossil record (Estes, 1981), and to date only four extinct taxa originally assigned to this group have been named and described in detail (Estes & Wake, 1972; Jenkins & Walsh, 1993; Evans & Sigogneau-Russell, 2001; Pardo *et al.*, 2017).

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 caecilians). Later, *Eocaecilia micropodia* Jenkins & Walsh, 1993, found in Lower Jurassic rocks of Arizona, 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, *Rubicacaecilia monbaroni* Evans & Sigogneau-Russell, 2001, was erected based on a nearly complete pseudodentary, with other isolated jaw elements, vertebrae, and a possible femur also attributed to it.

Chinlestegophis jenkinsi Pardo *et al.* 2017, from the Triassic of Colorado, 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 showing a combination of caecilian synapomorphies and lissamphibian plesiomorphies that suggests polyphyly of extant amphibians (Pardo *et al.* 2017). However, the close relationship of *Chinlestegophis* and gymnophionans 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).

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* suggested that similarities previously regarded as synapomorphies between the recumbirostran microsaur 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 poor, our present knowledge is sufficient to allow a more comprehensive approach, combining information from both extinct and extant taxa, to provide important clues to their past history. Here, we provide a review of the 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 caecilians.

4.1. Phylogeny and Classification of caecilians

The classification and definition of caecilian varies according to authors. Trueb & Cloutier (1991) proposed to restrict the names Apoda Oppel, 1811 for the crown-group of caecilians and Gymnophiona Rafinesque-Schmaltz, 1814 for the 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 changing it would probably bring more problems than create solutions. Thus, Marjanović & Laurin (2008a) proposed the term Gymnophionomorpha for a branch-based clade that comprises extant caecilians plus extinct taxa, such as *Eocaecilia micropodia* and *Rubricacaecilia monbaroni*.

According to the branch-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 11). Under the phylogeny proposed by Pardo *et al.* (2017), it would also include *Chinlestegophis jenkinsi*, and all other eryopiform temnospondyls (including stereospondyls and archeosaurids). On other phylogenies, members of the Gymnophionomorpha 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).

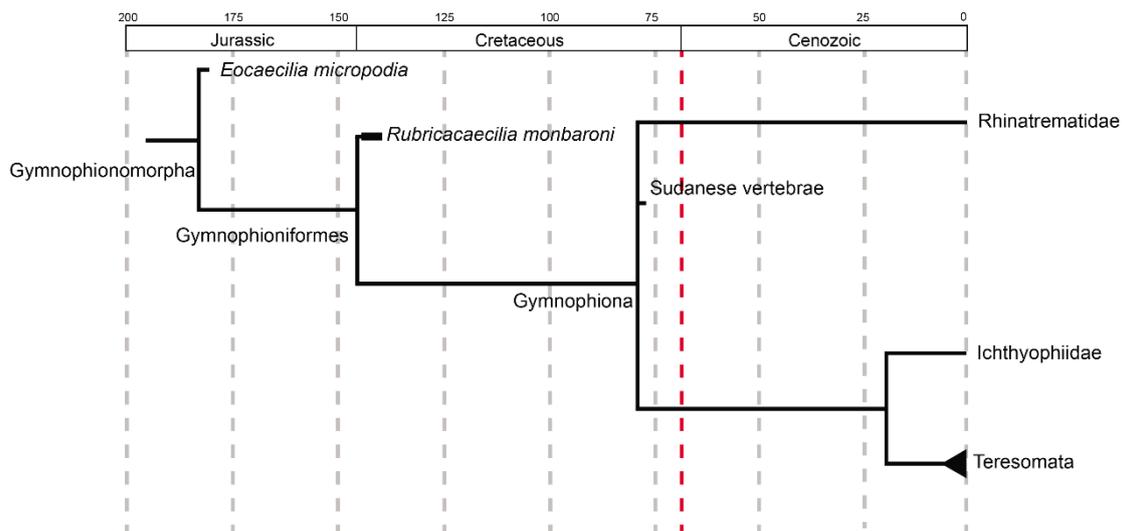


Figure 11: Time-calibrated phylogeny of Gymnophionomorpha, considering only paleontological data, including stem lineages plus the crown-group Gymnophiona, based on the topologies of Wilkinson *et al.* (2011) and Evans & Sigogneau-Russell (2001). Red stippled line indicates K-Pg boundary.

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 Anura and Urodela (e.g. Irisarri *et al.*, 2017). 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, morphological approaches designed to test the phylogenetic affinities of lissamphibians within an expanded taxon sample of Paleozoic tetrapods have resulted in fundamentally distinct hypotheses on the origin of the group (most recently reviewed in Marjanović & Laurin, 2019).

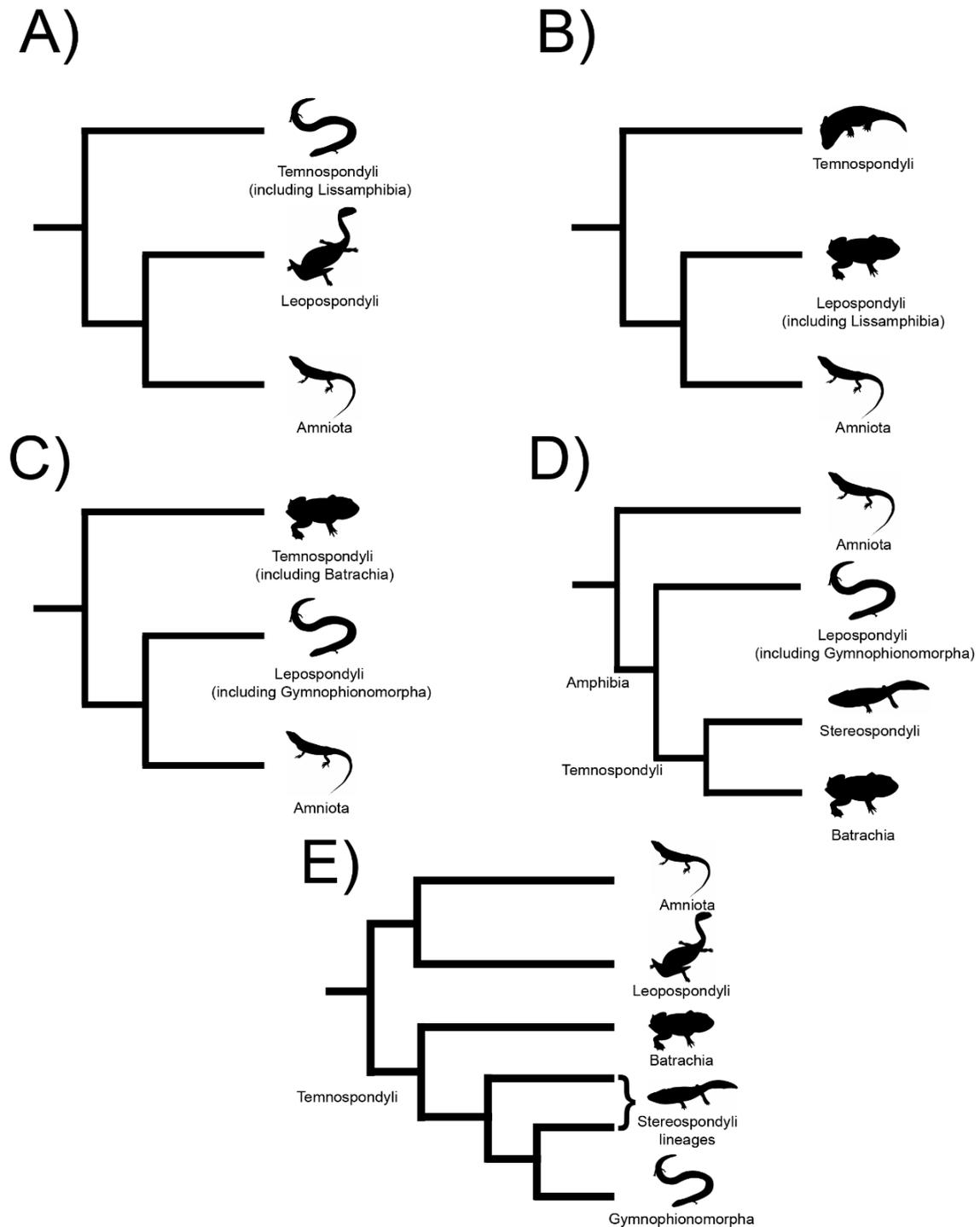


Figure 12: Different proposals for phylogenetic relationships of Lissamphibia, based on Marjanović & Laurin (2008a), Laurin *et al.* (2019) and Pardo *et al.* (2017). A) temnospondyl hypothesis. B) Lepospondyl hypothesis. C) One example of polyphyly hypothesis. D) Alternative version of the polyphyly hypothesis. E) Topology presented 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.

Currently there are three main phylogenetic hypotheses, all of which display minor variants (Figure 12). The first (Figure 12A) considers Lissamphibia a monophyletic group inside Temnospondyli (e.g. Trueb & Cloutier, 1991; Ruta & Coates, 2007). The second (Figure 12B) also recognizes monophyly of lissamphibians, but nested within Lepospondyli (e.g. Marjanović & Laurin, 2008a, 2009, 2019). The third (Figures 12C and 12D) suggests that extant amphibians do not actually form a monophyletic group, because frogs and salamanders are temnospondyls 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) gymnophionans are more closely related to amniotes than to batrachians, whereas this is contradicted by nearly all molecular (e.g. Irisarri *et al.*, 2017), total evidence (Pyron, 2011), and paleontological (Marjanović & Laurin, 2009, 2019) phylogenies.

The hypothesis recently proposed by Pardo *et al.* (2017) is compatible with molecular phylogenies in that the extant amphibians form a clade that excludes the amniotes (Figure 12E). According to this hypothesis, caecilians and batrachians had separate origins, with caecilians being nested among stereospondyls, whereas batrachians are dissorophoids. However, as shown by Marjanović & Laurin (2019) after a reanalysis of these data (including the modifications suggested by Dilkes, 2015), this topology is only one of four equally most parsimonious results. 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.

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, and molecular data, must be used to discriminate between the various hypotheses (e.g. Szostakiwskyj *et al.*, 2015).

4.2. Time Range of Gymnophionomorpha

Due to the limited nature of the amphibian fossil record (Figure 13), time divergence estimates 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 studies found a much

younger origin for amphibians, in the Permian, approximately 300–250 Ma ago (e.g. Marjanović & Laurin, 2007; 2008b).

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 age estimates are congruent with some previous divergence time estimates based on molecular data (e.g. Roelants *et al.*, 2007; Zhang & Wake, 2009; San Mauro, 2010), they are incompatible with others (e.g. Marjanović & Laurin, 2007). Although Pardo *et al.*'s (2017) estimates are compatible with the divergence times obtained from total-evidence tip dating by Pyron (2011), they are incompatible with the latter's topology. Clearly, Pardo *et al.* (2017) hypothesis has not been sufficiently corroborated to be considered well-supported.

The two other caecilian stem taxa, 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 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).

In summary, the gymnophionomorph fossil record is poor, consisting of stem-group taxa of Mesozoic age and fragmentary remains of Cenozoic crown-group taxa. This limited fossil record limits its use for molecular clock calibrations, and hinders interpretations of paleobiogeographical patterns.

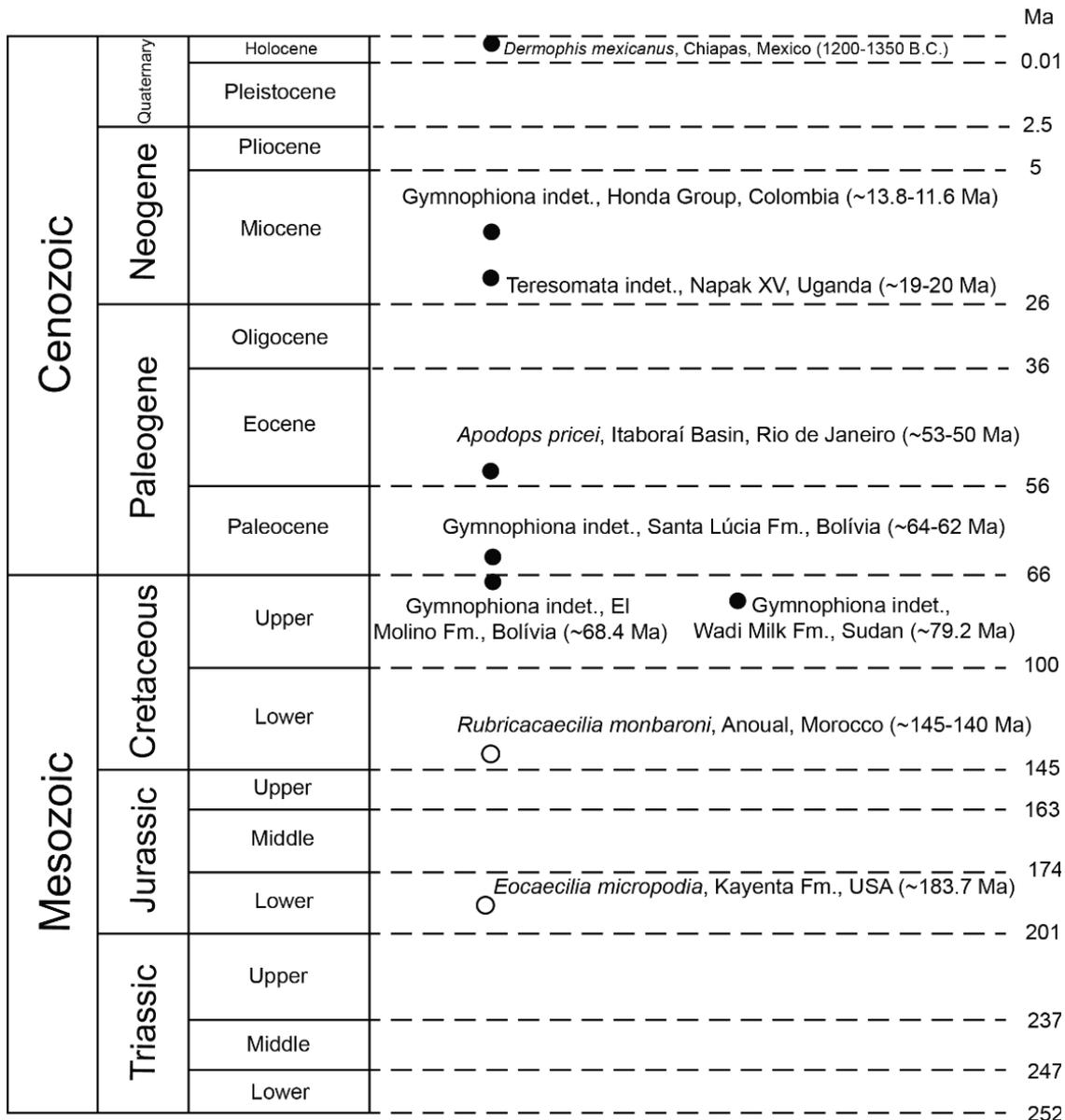


Figure 13: Summary of the fossil record of Gymnophionomorpha through geological time. Solid black circles indicate crown-group taxa, whereas circles with a black outline and white filling indicate stem-lineages.

4.3. Gymnophionomorpha Geographic Distribution

Extant caecilians have a pantropical distribution, occurring in South and Central 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 southern North America and northern Africa (Figure 14), regions not occupied by any extant caecilian.



Figure 14: Geographic distribution of extant caecilians, and fossil occurrences. Orange circles indicate stem-lineages, whereas white circles indicate crown-group taxa. 1) Forty specimens assigned to *Eocaecilia micropodia*, U.S.A. (Jenkins & Walsh, 1993). 2) Incomplete skull and postcranial elements assigned to *Rubicacaecilia monbaroni*, Morocco (Evans & Sigogneau-Russell, 2001). 3) Four vertebrae assigned to *Gymnophiona* indet., Sudan (Evans *et al.*, 1996). 4) Seven vertebrae assigned to *Gymnophiona* indet., Bolivia (Gayet *et al.*, 2001). 5) Isolated vertebra of *Gymnophiona* indet., Bolivia (Rage, 1991). 6) Single vertebra assigned to *Apodops pricei*, Brazil (Estes & Wake, 1972). 7) An incomplete skull assigned to *Teresomata* indet., Uganda (Rage & Pickford, 2011). 8) Three vertebrae assigned to *Gymnophiona* indet., Colombia (Hecht & Laduke, 1997). 9) One vertebra assigned to the extant species *Dermophis mexicanus*, Mexico (Wake *et al.*, 1999). Modified from Cogger & Zweifel (1998) and Loader *et al.* (2007).

Accounting for the gymnophionomorph fossil record at the beginning of the Mesozoic, a distribution at least in northern Pangea is well established (Pyron, 2014). However, either a northern origin followed by dispersal into Gondwana or a southern origin and subsequent radiation to Laurasia were proposed (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 Gondwanan distribution of extant taxa (Duellman & Trueb, 1994) and the Cretaceous record of *Rubicacaecilia monbaroni* (Evans & Sigogneau-Russell, 2001). However, the presence of *Eocaecilia* in North America raises the possibility of a Laurasian origin of Gymnophionomorpha.

Because of its paucity, the gymnophionomorph fossil record provides limited biogeographical data, and information from extant taxa, instead of fossils, are more helpful in evaluating biogeographic hypotheses (e.g. Gower *et al.*, 2002; Loader *et al.*, 2007).

4.4. Comparisons between extinct and extant Gymnophionomorpha

Chinlestegophis: a true gymnophionomorph?

The skull of the Triassic *Chinlestegophis jenkinsi* (Figure 15) 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 Triassic stereospondyls also occur in 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 separate supratemporal, postparietal, tabular and occipital bones, the presence of girdles, limbs, an otic notch, and a lateral-line sulcus (rarely present in lissamphibians nor in most lepospondyls), even though it is restricted only to the suborbital margins of the jugal and postorbital. An archaic os basale, comprising only exoccipitals and opisthotics, is also interpreted as being present in *C. jenkinsi* (Pardo *et al.*, 2017). However, 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; and saddle-shaped occipital condyles projected relatively far beyond the posterior margin of the skull. However, all these potential synapomorphies are problematic.

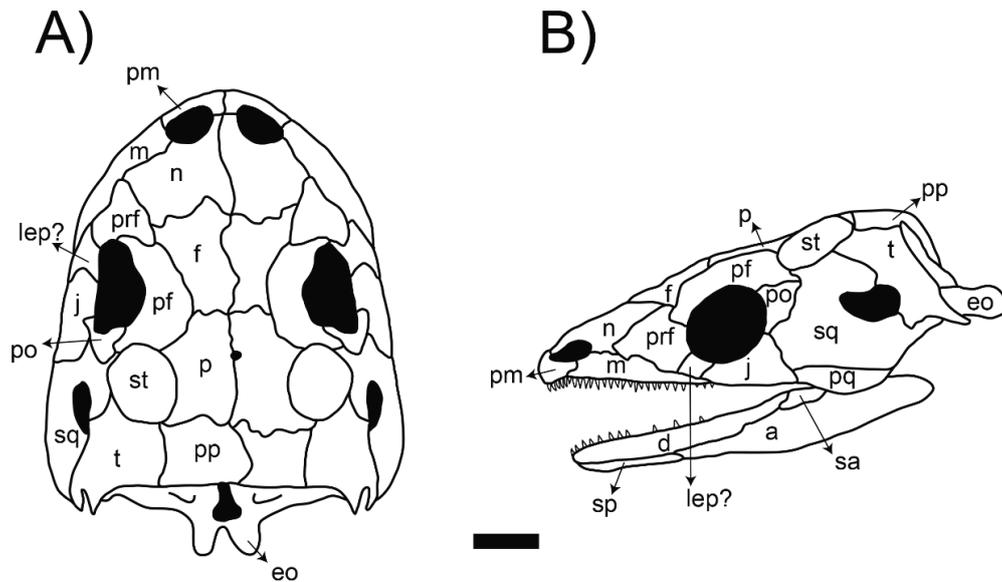


Figure 15: Reconstructions of the *Chinlestegophis jenkinsi* skulls in dorsal (A) and left lateral (B) views. Redrawn from Pardo *et al.* (2017). Abbreviations (for Figures 14, 15, 16, and 18): a, angular; ch, choana; d, dentary; dt, dorsal table; dta, dorsal tubercle of atlas; eo, exoccipital; f, frontal; 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; 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; rp, rostral process of parasphenoid; sa, surangular; sn, spinal nerve exit foramen; sp, splenial; spm, septomaxilla; sq, squamosal; st-q, stapes-quadrate; st, supratemporal; t, tabular; tig, tuberculum interglenoideum; to, tooth. Scale bar = 5 mm.

As Pardo *et al.* (2017) clarified 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*, 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) did not find one in any ontogenetic stage of *Dermophis mexicanus*, but Müller (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), a continuous coronoid tooth row evolved four times in stereospondyls then known: once in an unnamed clade that includes *Dvinosaurus*, *Tupilakosaurus* (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* plausibly 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.

Another claimed shared feature with caecilians is a broad cultriform process with parasagittal edges, but a similar condition is seen in lysorophians (Wellstead, 1991; Pardo & Anderson 2016), then this character has at least some degree of homoplasy. The saddle-shaped occipital condyles projecting relatively far beyond the posterior margin of the skull are visible in the skull of *Chinlestegophis jenkinsi*, but this character is present in many lepospondyls (Carroll & Gaskill, 1978), albanerpetids (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. Whereas 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), supported diphyly of extant amphibians, after modifications by Marjanović & Laurin (2009), it corroborated a monophyletic Lissamphibia originating among lepospondyls.

If *Chinlestegophis* were indeed closely related to caecilians, this would fill a major temporal gap in the fossil record of Gymnophionomorpha, according to the phylogeny of Pardo *et al.* (2017) another major gap would be created, on the batrachian stem, between the Early Permian Gerobatrachus and Batrachia. Lissamphibians also display a large gap in their fossil record under the lepospondyl hypothesis (Marjanović & Laurin, 2008b, 2009, 2013, 2019). Then, features of gymnophionans interpreted as adaptations for a fossorial lifestyle, including bone fusions and loss as well as reduction of limbs, girdles, and orbits appeared more gradually than previously thought. Note however that these characters are homoplastic and developed early in other lineages because they are present

in some Permo-Carboniferous lepospondyls (Carroll & Gaskill, 1978). In summary, there is sufficient uncertainty that the affinities of *Chinlestegophis* remain an open question.

4.5. Stem-Gymnophionomorpha

Several features in caecilian morphology, such as their stegokrotrophy (closed and compact skull structure, without temporal fenestrae), 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 caecilians, while rhinatrematids retain the plesiomorphic zygokrotrophic 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 stegokrotrophic skull (Jenkins & Walsh, 1993). According to the currently accepted topology illustrated in Figure 11, the closed skull roof of extant and stem caecilians evolved independently, and therefore the primitive condition of the crown group is zygokrotrophy (see Kleinteich *et al.*, 2012 for a more detailed discussion on this subject).

The distinct skull morphology of caecilians results from numerous bone fusion and/or loss events, forming a compact cranial structure well adapted for a head-first burrowing style of life (Nussbaum, 1983). We cite as examples the os basale (formed by the fusion of exoccipitals, opisthotics, prootics, parasphenoid, and basisphenoid), the maxillopalatine (comprising maxilla, palatine, and possibly lacrimal), the nasopremaxillae (formed by the nasals and premaxillae, but remaining as separate bones in some extant taxa), the pseudodentary (formed by the coronoid and dentary) 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 that clade's main diagnostic characters, especially limblessness. Subsequent 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.*, 2012a). The general skull morphology of *E. 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 (which may be a tabular), are primitive, because in gymnophionans, these bones were lost or incorporated into compound elements (Jenkins & Walsh, 1993). Additionally, some characteristics, such as a robust internal process in the lower jaw, are apparently unique for *Eocaecilia* (Jenkins *et al.*, 2007).

4.6. Stem-Gymnophioniformes

The fragmentary condition of the Cretaceous *Rubricacaecilia monbaroni* skull clouds morphological analyses, because only the palatine, pseudodentary, and pseudoangular are preserved. Unlike extant caecilians (Wilkinson *et al.*, 2011), but similarly to *Eocaecilia micropodia*, the palatine of *R. monbaroni* remains as a distinct bone not fused to the maxilla. However, contrary to *E. micropodia*, the number of inner teeth in the pseudodentary is reduced, as in some extant gymnophionans. As in 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 (e.g. Wilkinson *et al.*, 2011), and these 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. Whereas in *Chinlestegophis jenkinsi* the teeth are monocuspid and apparently not pedicellate (Pardo *et al.*, 2017), *E. micropodia* has bicuspid pedicellate teeth. Tooth morphology is poorly known in *Rubricacaecilia monbaroni*, because only the pedicels were preserved, but these clearly show that the teeth were pedicellate. The number of 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 zero in some ichthyophiids, dermophiids, and siphonopids (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 vertebral 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). *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 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* 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, the most obvious difference between stem and crown caecilians is the presence of limbs and girdles in the former and their complete absence in the latter. For *Chinlestegophis jenkinsi*, preserved disarticulated appendicular elements include a clavicle, interclavicle, and putative ulna; these are morphologically similar to those of other temnospondyls (Pardo *et al.*, 2017). For *Eocaecilia micropodia*, limb size is relatively reduced, a process that culminated in limblessness 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 on the presence of

trochanteric crest, a trait also observed in *E. micropodia* (Evans & Sigogneau-Russell, 2001).

4.7. 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, in having an amphicoelous and medially constricted centrum, wide parasphenes bearing large parapophysis, low and flat neural arch, short neural spine and a well-developed ventral keel (Wake, 1980). However, 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 (e.g. Wilkinson *et al.*, 2011). Therefore, the attribution of such fossils to Gymnophiona seems to be unequivocal, but 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 projecting 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 from Tiupampa described by Rage (1991) exhibits an amphicoelous centrum and well-developed parapophyses; however, it is too damaged to allow more precise identification.

Estes & Wake (1972) considered that the vertebra assigned to *Apodops pricei* closely resemble some extant genera from West Africa (*Geotrypetes*) and Central America (*Dermophis* and *Gymnopsis*) in morphology and proportions. The Colombian fossil vertebrae described by Hecht & LaDuke (1997) exhibit the typical caecilian morphology, except for size, which is 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 well-preserved condition, Rage & Pickford (2011) decided not 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 displays 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, the skull of Ugandan taxon is certainly not as zygokrotaphic as in *Scolecormorphus*. 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).

4.8. Systematic Paleontology

Tetrapoda Jaekel, 1909

Amphibia De Blainville, 1816

Gymnophionomorpha Marjanović & Laurin, 2008a

Eocaecilia micropodia Jenkins & Walsh, 1993

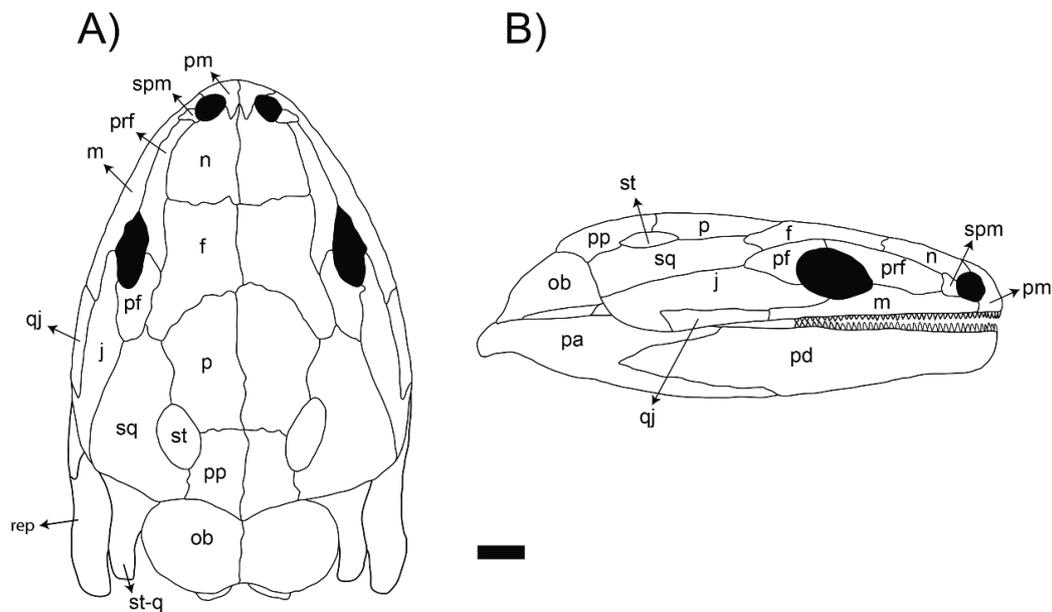


Figure 16: Reconstruction of *Eocaecilia micropodia* skull in dorsal (A) and right lateral (B) views. Redrawn from Jenkins *et al.* (2007). See Figure 15 for abbreviations. Scale bar = 1 mm.

Hypodigm: Forty 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.*, 2012a).

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

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

Main characteristics: *Eocaecilia micropodia* was the first stem-caecilian described. Of the 40 specimens assigned to this species, two are almost complete skulls (Figure 16). 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 with the tentacle), a complete os basale (formed by the fusion of six bones, namely the supraoccipital, exoccipital, basisphenoid, basioccipital, pleurospenoid, and parasphenoid), and a lower jaw formed by pseudoangular and pseudodentary.

Observed ancestral traits include 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 small, possibly indicating specialization towards fossorial behavior. Uniquely derived characters comprise the presence of a fused stapes-quadrate, an oblique and almost planar jaw joint, a robust internal process of the lower jaw projected towards the adductor chamber, and a higher total number of teeth.

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

Rubricacaecilia monbaroni Evans & Sigogneau-Russell, 2001

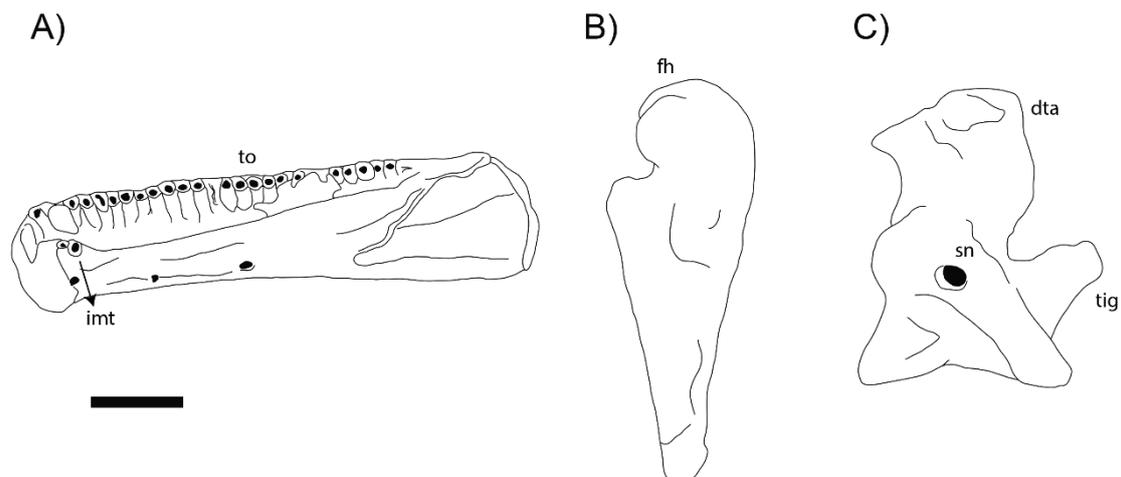


Figure 17: Drawings of *Rubricacaecilia monbaroni* holotype, a right pseudodentary (MCM 171) in lingual view (A), proximal head of a left femur (MCM 3) tentatively referred to the species (B), and referred atlas (MCM 175) in right lateral view (C). Redrawn from Evans & Sigogneau-Russell (2001). See Figure 15 for abbreviations. Scale bar = 1 mm.

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

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 17), despite their fragmentary nature, reveal a morphology consistent with an ancient stem-caecilian. Among its primitive characters, there is no anterior process on the parasphenes, whereas such a process is found in all extant caecilians. Other 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 on the atlas.

Unlike extant caecilians, but like *Eocaecilia micropodia* and *Chinlestegophis jenkinsi*, *Rubricacaecilia monbaroni* also bears a toothed palatine separate 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 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) interpreted *Rubricacaecilia monbaroni* as a stem-caecilian, more closely related to the crown groups than is *Eocaecilia micropodia*, but considered that its incompleteness and the tentative association of some materials justified not carrying out a phylogenetic analysis, which could test this hypothesis. Therefore, the relationship between *Rubricacaecilia* and the other gymnophionomorphans must be interpreted with caution until a cladistic analysis that includes it is carried out.

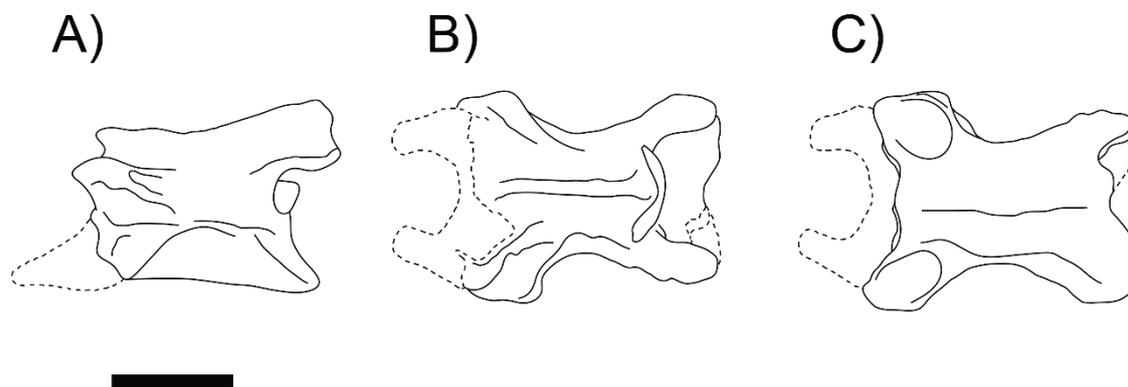
Apodops pricei Estes & Wake, 1972

Figure 18: Holotype precloacal vertebra (DGM 551) of *Apodops pricei* in left lateral (A), ventral (B) and dorsal (C) views. Missing parts indicated with stippled lines. Redrawn from Estes & Wake (1972). Scale bar = 1 mm.

Holotype: the holotype (DGM 551) is limited to a single trunk vertebra (Estes & Wake, 1972; Estes, 1981), previously 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: *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 18), lacking only parts of prezygapophyses, parapophyses, and the posterior edge of the neural arch, closely resembles 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 projecting basapophyses.

Besides the well-developed ventral spine, the amphicoelous centrum also exhibits a pronounced medial constriction. Even though most of both parapophyses were lost during the fossilization process, their broad bases can be used to infer the 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 grooves that extend 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). 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 extensive ossification, a long and deep ventral keel, and deep blood vessel grooves were uniquely derived and, therefore, erected a new genus and species for it. Subsequently, Taylor (1977) described some vertebrae of *Siphonops*, an extant caecilian 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*.

These structures are not unique among caecilians, and such variations can also be related to the position of vertebra along the column or ontogeny (Wake, 1980). 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 have subsequently been described but none was used to erect new species. Therefore, the designation of *A. pricei* as a valid species needs to be reevaluated. However, this is out of the scope of this work.

4.9. *Teresomata* indet.

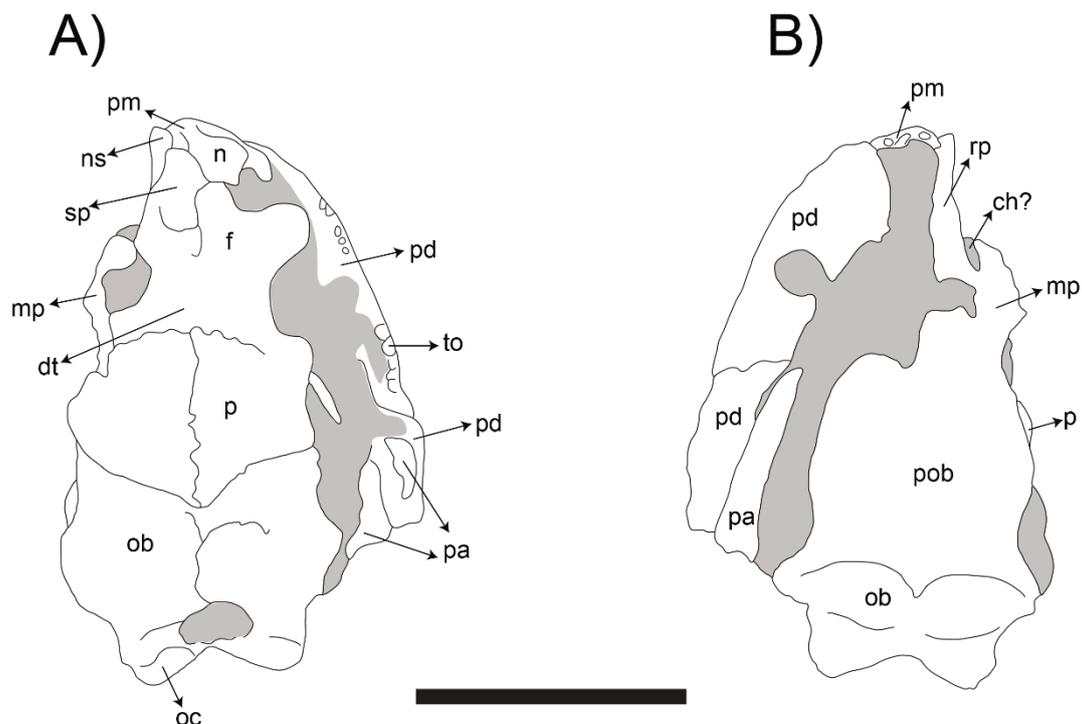


Figure 19: *Teresomata* indet. incomplete skull and right lower jaw (Nap XV 148'08), in dorsal (A) and ventral (B). Areas covered by rock are indicated in grey. Redrawn from Rage & Pickford (2011) and Gardner & Rage (2016). See Figure 15 for abbreviations. Scale bar = 1 cm.

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 vertebral material, with one exception: a partial skull with articulated lower jaw from the Miocene of Uganda (Figure 19). 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 in the occipital region).

In the original description, a single compressed bone, named 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 anurans (sometimes the bone is called the frontoparietal), would be unique among caecilians, because all of them exhibit separated parietals and frontals. However, based on the published images, a suture can be observed partially delimiting the parietals and the frontals. Notches on either side of the frontals, are the dorsalmost portions of the orbital margins. The compact skull structure implies a stegokrotaphic skull or the presence of a narrow upper temporal fenestrae. Posteriorly, the specimen preserves the parasphenoid portion of the os basale and two occipital condyles. Only anterior fragments of a pseudodentary (including some cross sections of marginal teeth) and parts of anterodorsal and anteroventral processes of the pseudoangular are preserved. Between these two bones lies a long and oblique suture.

Remarks: Specimen Nap XV 148'08 was provisionally referred to Caeciliidae sensu Frost *et al.* (2006), a group equivalent to the Teresomata of Wilkinson & Nussbaum (2006). Given that some portions of the skull remain embedded in the matrix, further preparation and imaging (i.e. CT scanning), may help to reveal additional phylogenetic characters.

4.10. *Gymnophiona* 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 (MHNC-2635, housed at the Museo de Historia Natural de

Cochabamba) and 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; 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; middle Maastrichtian (~68.4 Ma) and early Paleocene (~64–62 Ma) for Bolivian material, middle Miocene (~13.8–11.6 Ma) for Colombian fossils, and Quaternary (1200–1350 B.C.) for Mexican fossil.

Main characteristics: Morphologically, the caecilian 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, no examples of these vertebrae are known for published fossil crown-caecilians. Therefore, due to the lack of more specific diagnostic characters, all of the above-listed fossil vertebrae can only be assigned to *Gymnophiona* indet.

4.11. Unpublished and possible indeterminate record

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). 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 for Maboko Island, Kenya, originally published by Andrews *et al.* (1981, table 1), a record assigned to a Miocene neotridian was reported, but without images or detailed descriptions. Due to the significant temporal gap that this record would imply in the neotridian fossil record (neotridians 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 neotridian assignment.

4.12. Possible calibration constraints for Gymnophionomorpha

Calibration constraints based on the caecilian fossil record are uncommon, probably because 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), and based on our review of the caecilian fossil record, we provide calibrations for three nodes of the gymnophionomorphans. We attempted to use the most recent or widely accepted age estimates for each location. Calibrations are highly dependent on phylogeny and stratigraphy, and thus the latest, best-supported dating and phylogenetic hypotheses were considered.

GYMNOPHIONOMORPHA Marjanovic & Laurin, 2008a

Assuming monophyly of Lissamphibia

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).

Phylogenetic Justification: If lissamphibians and batrachians are both monophyletic, then the age of Batrachia and Gymnophionomorpha is the same. In this scenario, the oldest

fossil available is the stem-batrachian *Triadobatrachus*, from the Early Triassic of Madagascar.

Minimum age: 251.2 Ma

Soft Maximum age: 254.1 Ma

Age Justification: Traditionally, estimates for the age of the Sakamena Group in Madagascar range from the Late Permian to the Middle Triassic. However, due to the absence of radiometric and magnetostratigraphic dating, age estimates are inaccurate (Benton *et al.*, 2015). Based on palynological evidence, a Changhsingian-Induan age was proposed for this unit (e.g. Wescott & Diggins, 1998; Nowak *et al.*, 2018).

Assuming a diphyletic origin of Lissamphibia

Node Calibration: Divergence between Gymnophionomorpha and *Rhynchonkos stovalli* (Olson, 1970)

Oldest fossil: *Rhynchonkos stovalli* (Olson, 1970), from Fairmont Shale (Early Permian), Hennessey Group, Oklahoma, USA (the holotype comprises a complete and articulated skull).

Phylogenetic Justification: Considering a diphyletic hypothesis for the origin of lissamphibians (e.g. Anderson *et al.*, 2008) and the branch-based definition of Gymnophionomorpha presented by Marjanovic & Laurin (2008a), the oldest fossil available is *Rhynchonkos stovalli*

Minimum age: 272.9 Ma

Soft Maximum age: 283.5 Ma

Age Justification: *Rhynchonkos* comes from Norman locality, initially considered part of Hennessey Formation (Annadarko Basin), but posteriorly this unit was subdivided into Fairmont Shale, Kingmont Siltstone, and Salt Plains Formations (Becker *et al.*, 1997). The outcrops of Fairmont Shale in the Norman locality are considered to be laterally equivalent to the better known Choza Formation (Olson, 1970), and thus Kungurian in age based on biostratigraphic dating (e.g. Tharalson, 1984; Nelson *et al.*, 2013).

Comments: According to some paleontological and molecular evidence (e.g. Marjanovic & Laurin, 2007; Anderson *et al.*, 2008; Pyron, 2011; Pardo *et al.*, 2017), the origin of Lissamphibia dates from the Permian or even late Carboniferous. Considering the topology of Pardo *et al.* (2017), numerous temnospondyls (such as “amphibamids”, dissorophids, and stereospondyls) also fall within the lissamphibian crown clade, with late Carboniferous taxa like *Amphibamus* and *Platyrrhinops* being among the oldest

available fossils that could be used to constrain the Gymnophionomorpha age in ~315 Ma. However, as discussed above, this hypothesis still needs to be evaluated.

GYMNOPHIONA Rafinesque-Schmaltz, 1814

Node Calibration: Divergence between Rhinatrematidae Nussbaum, 1977 and Stegokrotaphia Cannatella & Hillis, 1993.

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 anteroventrally.

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 deposited in flood plains, lakes, and meandering rivers. Historically, it was considered to be Albian-Santonian in age, on the basis of palynological evidence (Schank, 1990). However, recent U-Pb radiometric dating found a much younger age of: 79.2 ± 2.4 Ma, or equivalent to the middle Campanian (Agyemang *et al.*, 2019).

Comment: Previously, Benton *et al.* (2015) proposed a Paleogene minimum age for *Gymnophiona*, based on the record of *Apodops*. The Sudanese vertebrae share with crown-gymnophionans the presence of well-developed parapophyses, which are absent in both *Eocaecilia* and *Rubricacaecilia*, and this support pushing the temporal range of crown-*Gymnophiona* back to the middle Campanian. However, this remains tentative, because the Sudanese taxon 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.

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

Phylogenetic Justification: As Nap XV 148'08 has not yet been included in phylogenetic analyses, its affinities are still uncertain, and 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

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 older unnamed fossil caecilians from the early Paleocene (Rage, 1991) and Maastrichtian (Gayet *et al.*, 2001) of Bolivia, and Campanian of Sudan (Evans *et al.*, 1996) to Teresomata. Therefore, the oldest fossil that can be undoubtedly assigned to this clade is the skull Nap XV 148'08.

4.13. Conclusions

Gymnophionans 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 assignable to the caecilian crown-group would likely make a substantial contribution to resolving phylogenetic and biogeographic questions and better constraining molecular clocks.

5. Material and Methods

5.1. Analyzed specimens

The specimen described in the present study, DGM 1462-R (Figure 20), is part of the Museu de Ciências da Terra collection, under the acronym DGM (Divisão de Geologia e Mineralogia). Three species of modern caecilians, *Siphonops paulensis*, *Chthonerpeton indistinctum* and *Caecilia tentaculata*, from the herpetology collection of Museu de Zoologia da Universidade de São Paulo, were also used for morphological comparison purposes.



Figure 20: The specimen DGM 1462-R. Scale bar = 1 cm.

5.2. Collection area

The specimen DGM 1462-R comes from an outcrop of assigned to the Taubaté Basin (Tremembé Formation), located in an area belonging to Sociedade Extrativa Santa Fé LTDA (Figure 21), in the neighborhood of Padre Eterno, municipality of Tremembé, approximately 13 km north of Taubaté city.



Figure 21: Shale (in blue) and greenish mudstone (in red) layers of Tremembé Formation at Fazenda Santa Fé, in 2005. Retrieved from Ribeiro (2010). Photo by H. Alvarenga.

5.3. Morphological Description Terminology and Taxonomic Assignments

Morphological descriptions of the skull and postcranial characteristics of DGM 1462-R follow the terminology and methodology employed by Taylor (1977); Wake (1980); Nussbaum & Wilkinson (1989); Wilkinson & Nussbaum (1997; 1999), Jenkins *et al.* (2007). Taxonomic assignments of all observed specimens were based in the features defined by Wilkinson & Nussbaum (1997; 1999; 2006) and Wilkinson *et al.* (2011).

5.4. CT Scan and image processing

The specimen DGM 1462-R was submitted to CT-scanning procedures on a 300-kV μ -focus X-ray source micro computed tomography GE Phoenix v|tome|x M 300

(General Electric Measurement & Control Solutions, Wunstorf, Germany), located at the Laboratório de Microtomografia of the Museu de Zoologia in the Universidade de São Paulo. The parameters used in scans (e.g. time of exposure, number of projections, kilovoltage and current strength) were defined in order to obtain the best results in terms of spatial resolution and image contrast. Attempting to improve the resolution, a Multiscan including 5 individual scans of the whole body was performed. The voxel size is 34 μm , voltage is 160 kV, current is 120 μA .

After these procedures, the data were processed on a workstation composed by a HP Z820 computer equipped with eight-core Intel Xeon E5-2660, 2.20 GHz (2 processors), 128 GB of memory and running Windows 7 Ultimate 64 bit with a graphics processing unit Cubix Elite Xpander (Cubix Corporation, Carson City, NV). Then, such raw data were reconstructed through the software phoenix dataview reconstruction v. 2.3.0 (General Electric Measurement & Control Solutions, Wunstorf, Germany). The visualization of 3D files and the analysis of the reconstructed data were executed in VGStudio MAX 2.2.3 64 bit (Volume Graphics GmbH, Heidelberg, Germany) and also in the MeshLab software, where the "Measuring Tool" was used to collect data of Table 1.

5.5. Phylogenetic analyses

A phylogenetic parsimony analysis was performed using the 1.5 version of the software TNT (Goloboff & Catalano, 2016), with a dataset containing 60 morphological characters coded for 38 taxa. The analyses were conducted adopting the heuristic Traditional Search algorithm of multiple Random Addition Sequence (RAS), with 5000 replicates, followed by branch swapping (Tree Bisection and Reconnection) with the option "collapse all trees after the search" on.

The Consistency (Kluge & Farris, 1969) and Retention (Farris, 1989) indexes were calculated using the "wstats.run" script. The Bremer Support (Bremer, 1994) values were estimated saving suboptimal trees for additional step intervals (1, 3, 5, 7, and 10) and then using the option "Bremer Supports" of T.N.T. Bootstrap (Felsenstein, 1985) was calculated using 10000 replicates and the standard option (sample with replacements) selected. Jackknife (Farris *et al.*, 1996) was performed also with 10000 replicates and selecting the option "removal probability = 36".

The “Traditional” data matrix of Wilkinson (1997) was adopted, with minor modifications. A typographic error in character 8 (T8 in the original analyses) was fixed. States of character 16 (20b in the original work) were changed from 1 to 0 in *Epicrionops bicolor* and *Epicrionops petersi*. Character 28 (T31 in Wilkinson matrix), was also modified by coding the character state “transverse” as 1 and “circular” as 2 in the matrix. The new characters added to the matrix of Wilkinson & Nussbaum (1999) were detailed in the Appendix.

A total of 12 OTU’s were added to the original data matrix, including *Rhinatrema bivittatum*; *Ichthyophis bannanicus*; *Chikila fuller*; *Typhlonectes compressicauda*; *Nectocaecilia petersi*; *Potomotyphlus kaupii*; *Atretochoana eiselti*; *Siphonops paulensis*; *Caecilia tentaculata*; *Caecilia gracilis*; *Herpele squalostoma* and *Praslinia cooperi* and the specimen DGM 1462-R.

6. Results

6.1. Systematic Paleontology

Amphibia De Blainville, 1816

Gymnophionomorpha Marjanović & Laurin, 2008a

Gymnophiona Rafinesque-Schmaltz, 1814

Teresomata Wilkinson & Nussbaum, 2006

Typhlonectidae Taylor, 1968

6.2. General description

The DGM 1462-R material comprises the anterior region of a fossil caecilian (Figure 22), including skull bones and vertebrae still articulated. The specimen is divided into two plates, one with the dorsal portion and the other with the ventral one. Diagnostic characteristics associated with *Gymnophiona* include the presence of pseudangular, pseudodentary, os basale, elongated body, amphicoelous vertebrae with well-developed parasphenes and the absence of both limbs, pectoral and pelvic girdles.

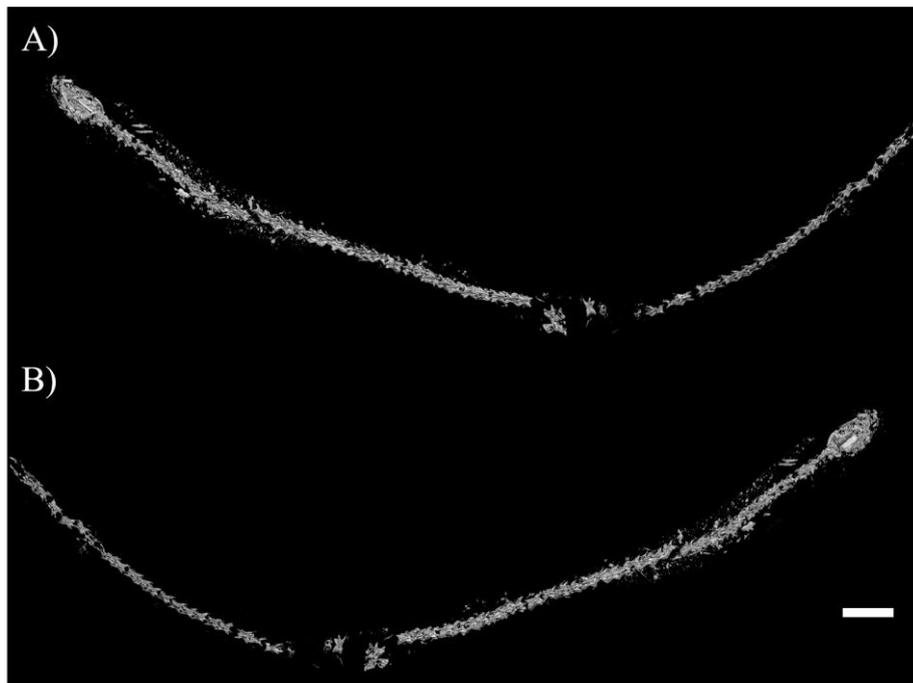


Figure 22: CT-scan of DGM 1462-R, in ventral (A) and dorsal (B) views. Scale bar = 1 cm.

6.3. Skull

The skull (Figure 23) is fragmented and compressed, with most bones broken into short or indistinct fragments, with the exception of both parietals and the left pseudangular. Although severely damaged, some fragments were recognized and tentatively associated to the frontals, pseudodentaries and the posteroventral portions of the os basale, along with some teeth crowns separated or not from their pedicels, as well as other unidentified bone fragments.

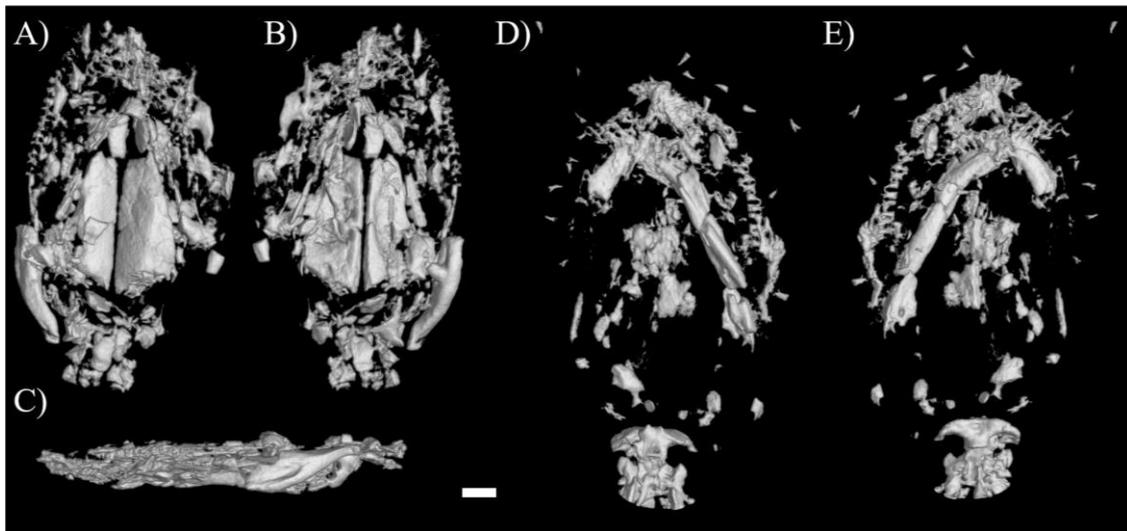


Figure 23: CT-scan of the two skull parts of DGM 1462-R. The first part in dorsal (A), ventral (B), and lateral views (C), and the second part in dorsal (D) and ventral (E) views. Scale bar = 1 cm.

6.3.1. Parietals

The parietals (Figure 24) are the best-preserved bones in the DGM 1462-specimen. Both are almost complete, however a small dorsolateral portion of the left one is missing. They have a roughly trapezoidal outline in dorsal view, except for an anterolateral pointed corner. The dorsal surface is smooth and flat, except in the posterolateral margins, in which a pronounced slope ventrally oriented is present. Ornamentations in form of small grooves at the dorsal surface are lacking, while the ventral surface remains covered by a portion of the os basale, which collapsed over them during the fossilization.

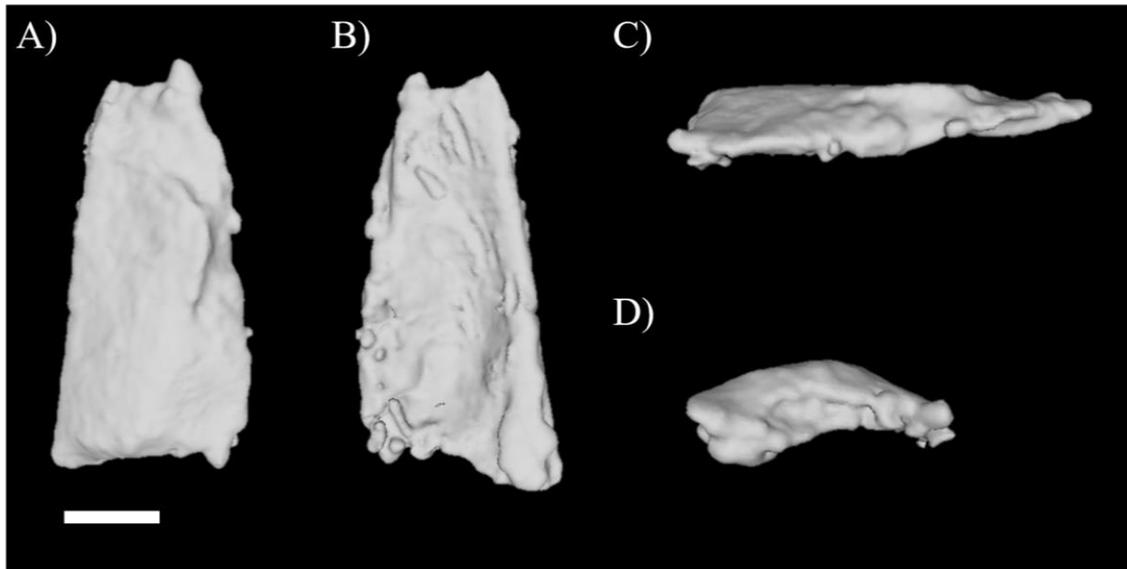


Figure 24: Right parietal in dorsal (A), ventral (B), lateral (C), and posterior (D) views. Scale bar = 1 mm.

6.3.2 Frontals

Two bone fragments, located anterior to both parietals, were tentatively identified as the frontals. Despite being preserved, they are substantially damaged, showing an irregular shape. However, based on the shape of the anterior margin of the parietals and the outline of these fragments, their posterior margin is roughly straight.

6.3.3. Os basale

Numerous fragments located in the posterior portion of the skull were associated to different parts of the os basale (Figure 25). One of these fragments, located immediately behind the pseudangular, comprises the os basale lateral wall. In lateral view, there are 2 partially preserved foramina. The precise identification of these foramina is difficult, because the caecilian os basale bears numerous different foramina, such as foramen ovalis, jugular foramen, and antotic foramina (Maddin, 2011). The anteriormost foramen is larger, but is incomplete, as its anterodorsal margin is lacking. Posterodorsal to it and separated only by a thick bone layer, lies the other foramen. Posteriorly to these foramina there is a crest projecting posterolaterally.

Other fragments are collapsed on the parietals, and the association with the os basale, identified through the presence of the right carotid foramen. In addition to these, other fragments also belonging to the os basale are scattered throughout the posterior

region of the skull, but their poor state of preservation, which difficult the visualization of diagnostic structures, hinders a better characterization of the material.

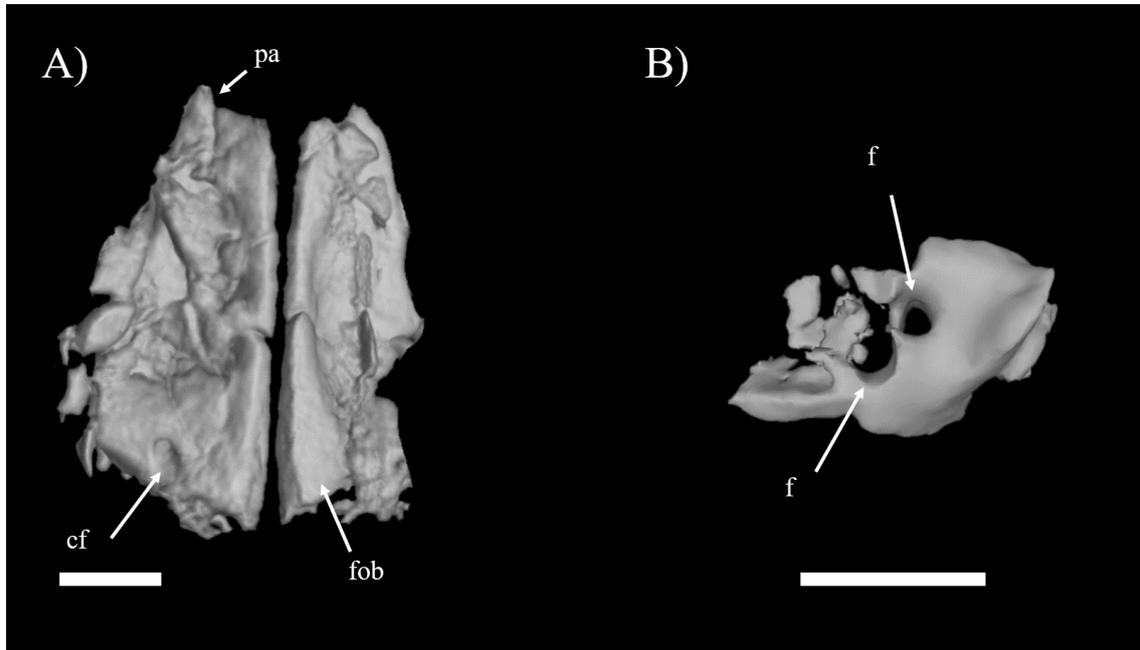


Figure 25: Fragments associated to os basale collapsed on the parietals in ventral view (A) and the antotic region in lateral view (B). Abbreviations: cf: carotid foramen; f: foramen; fob: fragments of os basale; pa: parietal. Scale bar = 1 mm.

6.3.4. Lower jaw

Posteriorly, the pseudangular (Figure 26) is one of the bones that forms the caecilian jaw. In the DGM 1462-R specimen, only the left was fully preserved. In lateral view, this bone bears a posteriorly recurved retroarticular process, with a well-developed lateral crest, but with a marked notch on its posterodistal margin. The suture between it and the pseudodentary is excavated in the anterior margin and its concave surface has a roughly triangular and narrow shape. A dorsally directed processus condyloides is not present. Indeed, it is not possible to distinguish it in this view. In the dorsal view, the articular surface is curved and surrounded posteriorly by the processus condyloides (restricted to a short lift) and anteriorly to a flat surface, without evidence of a preserved canalis primordialis. The internal process is anteromedially directed and has a roughly quadrangular outline, and the retroarticular process is curved posteromedially. In medial view, the most distinctive features are the foramina of the ramus intermandibularis. One is located at the posterior base of the internal process, whereas the other is excavated

anteriorly to this process. In the anterior view, the channel for the passage of the ramus intermandibularis is conspicuous due to the pseudangular fragmentation.

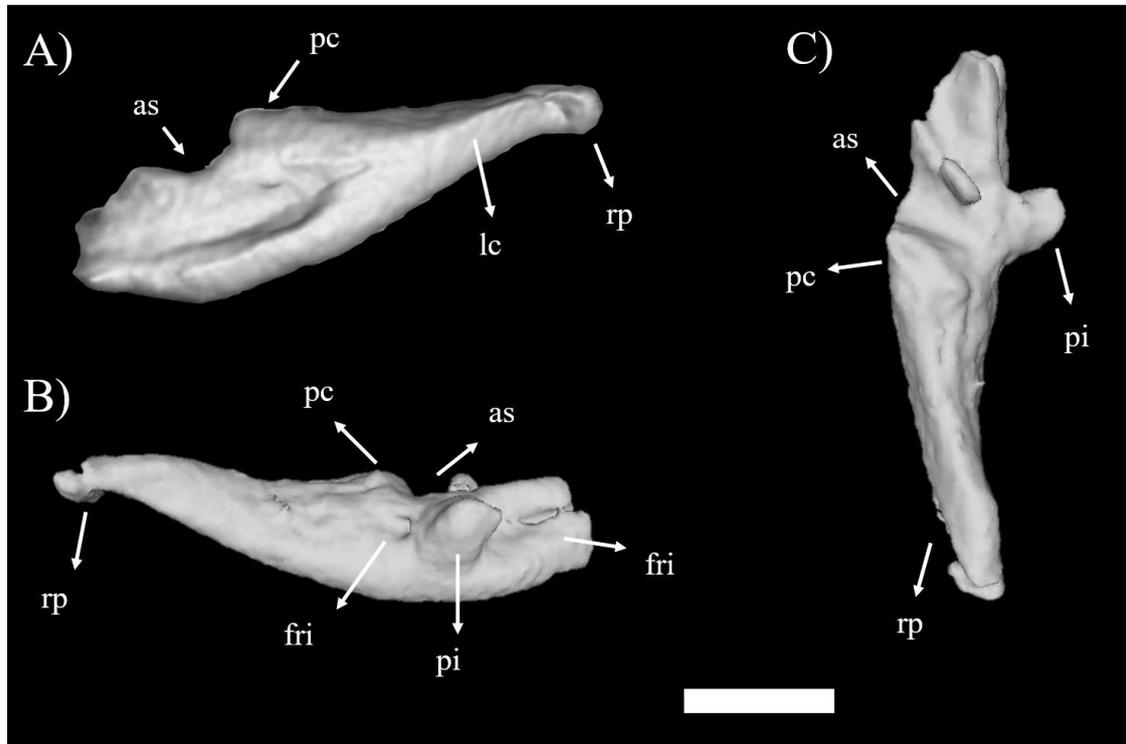


Figure 26: Left Pseudangular in lateral (A), lingual (B), and dorsal (C) views. Abbreviations: as: articular surface; fri: foramen for the ramus intermandibularis; lc: lateral crest; pc: processus condyloides; pi: processus internus; rp: retroarticular process. Scale bar = 1 mm.

Both pseudodontaries have been preserved, yet severely fragmented. In the right one, only the portion closest to the mandibular symphysis was preserved, while the left one, although broken into three fragments, extends more distally almost reaching the contact region with the pseudangular. They are elongated anteroposteriorly and flattened laterally, with a slight dorsolateral curvature. There are no signs of pedicels attached to the bones and, therefore, it is not possible to determine the presence of splenial teeth.

6.3.5. Dentition

A total of 18 crowns of teeth, separated or not from their pedicels, were recognized in the DGM 1462-R specimen. These crowns exhibit a simple morphology, with only a single conical and curved cusp, with a pointed apex and without evidence of lateral flanges. Although it is not possible to count the exact total teeth number, the arrangement of the pedicels makes it possible to observe the presence of the typical caecilian

concentric double teeth row. The size of the crown of the teeth varies slightly, but is approximately 0.5 mm for the most.

6.4. Postcranium

The post-cranial portion of DGM 1462-R consists in a fragmented atlas, still articulated to the skull, followed by the other vertebrae (most also articulated with each other, although in the median portion of the specimen they are scattered) and some ribs. Since the most caudal region of the body was not preserved, the specimen is restricted to the anterior portion of the body.

6.4.1. Atlas

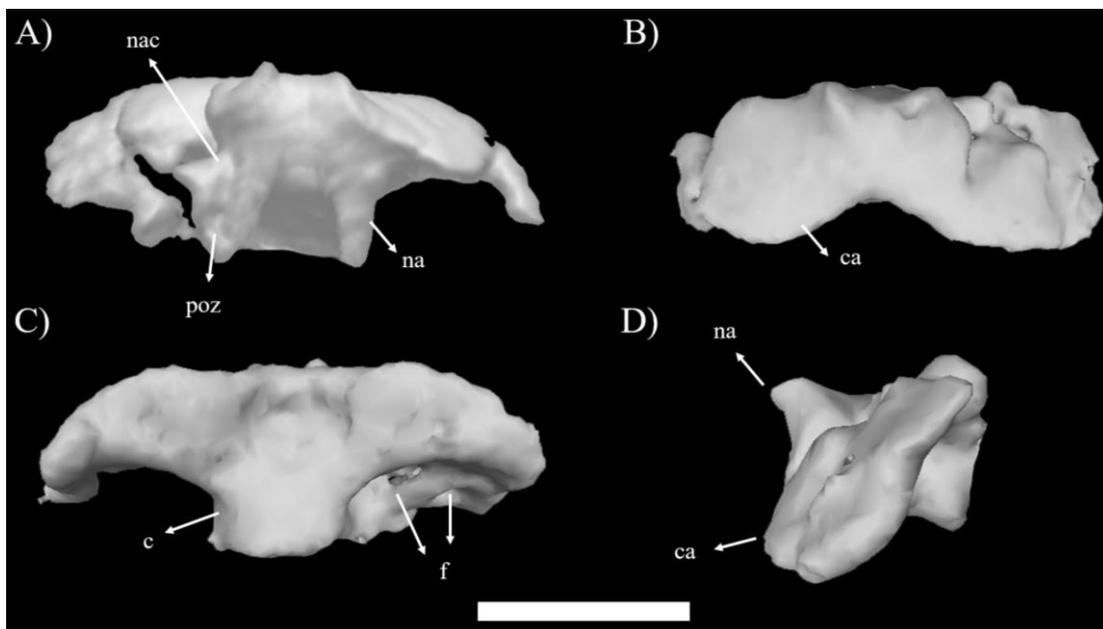


Figure 27: Atlas in dorsal (A), anterior (B), ventral (C), and lateral (D) views. Abbreviations: c: centrum; ca: cótyles of atlas; f: foramina; na: neural arches; nac: neural arch constriction; poz: postzygapophysis. Scale bar = 1 mm.

The Atlas (Figure 27) is damaged, but preserves some important diagnostic features. The two atlantal cotyles were preserved, although the upper portion is fragmented. They have an anteroposterior slope and a relatively flat anterior surface. The cotyles are fused anteriorly, but there is a slight constriction between them. There are 2 foramina on the posterior face of the right cotyle, but on the left one this portion is absent, and thus the presence of these structures cannot be determined with certainty. The neural arch is almost completely absent, except for portions on its anterior margin bases and just anterior to the postzygapophyses. These two bases show that the halves of the neural arch

are separated ventrally by a diastema. A pronounced constriction is present in the portion just anterior to the postzygapophyses. The length of the vertebral center is significantly shorter compared to the following vertebrae. The ventral surface of the centrum is smooth, with no evidence of ventral keel. The atlas does not bear ribs.

6.4.2 Second Vertebra

The second vertebra (Figure 28) is articulated to the atlas, but it is so fragmented that few features can be securely identified. The neural arch was compressed and collapsed. Both prezygapophyses are present, showing a flat articular surface. On the left one, two foramina are present. The vertebral centrum has a pronounced keel on its ventral surface. No ribs were recognized.

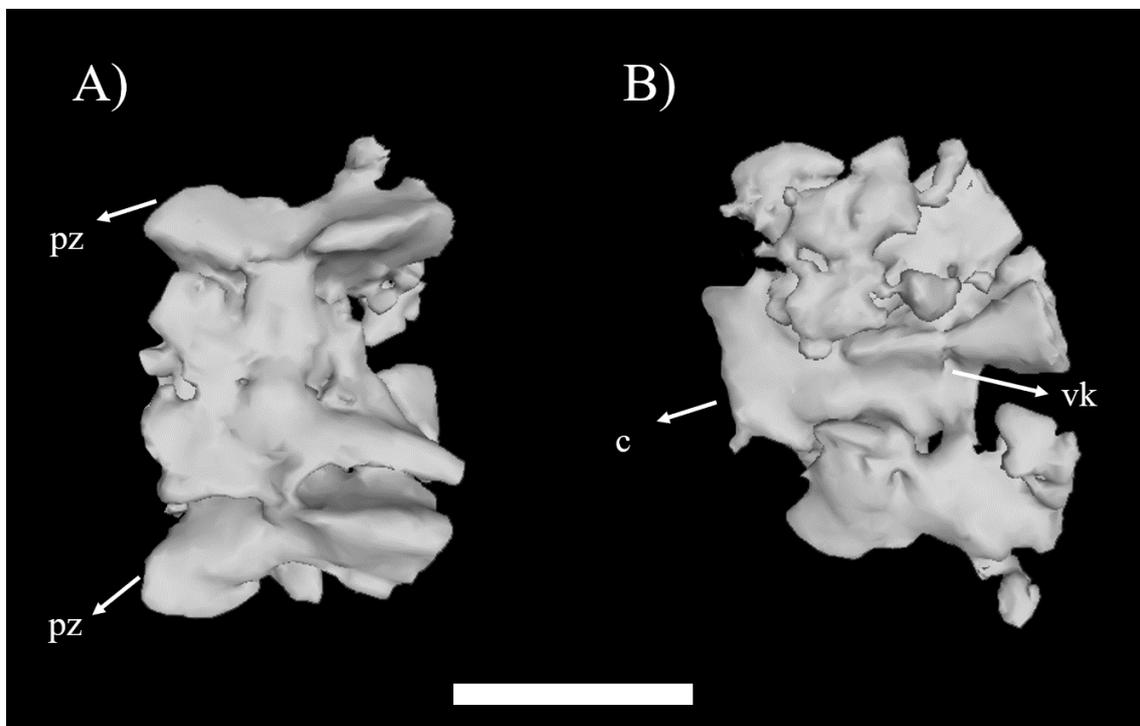


Figure 28: Second vertebra in dorsal (A) and ventral (B) views. Abbreviations: c: centrum; pz: prezygapophyses; vk: ventral keel. Scale bar = 1 mm.

6.4.3. Vertebrae

The remaining vertebrae show a similar morphology between each other, with few variations in size and/or shape. At least 54 vertebrae were identified, since some are so fragmented that they are hardly individualized from each other. All vertebrae have a degree of dorsoventral compression. In general, the vertebrae exhibit an amphicoelous

centra with a lateral constriction, well-developed parasphenes projected anteroventrally, a pronounced ventral keel, and low neural arches.

Due to the compression and fragmentation of the specimen, the presence of nuchal crests in the anterior vertebrae is difficult to evaluate. However, in some well-preserved posterior trunk vertebrae (Figure 30), the nuchal crest is present, but it is very weak. The parasphenes of the trunk vertebrae bear, on their ventral surface, pronounced ridges. According to the ratios of Table 1, the vertebrae have an anteroposterior elongation in a similar degree, but not marked as in *Typhlonectes*, and this feature is more conspicuous in the distal trunk vertebrae.

Table 1: Values of the ratio between the total vertebral length (distance from the parapophysis to the postzygapophysis) and the total width (distance between the postzygapophyses). Values of DGM 1462-R are based on the vertebra of Figure 29 (around 40th position in the column). A) 20th vertebra. B) 50th vertebra. Other values were based on the data of Peter (1894), Estes & Wake, 1972 and Wake (1980).

Táxon	Ratio W/L
DGM 1462 R	0.50
<i>Typhlonectes natans</i> (A)	0.51
<i>Typhlonectes natans</i> (B)	0.46
<i>Typhlonectes compressicauda</i>	0.46
<i>Geotrypetes seraphinii</i>	0.60
<i>Chthonerpeton indistinctum</i>	0.54
<i>Dermophis mexicanus</i>	0.94
<i>Gymnopsis multiplicata</i>	0.66
<i>Hypogeophis rostratus</i>	0.58
<i>Schistometopum thomense</i>	0.57
<i>Ichthyophis glutinosus</i> (A)	0.57
<i>Ichthyophis glutinosus</i> (B)	0.56

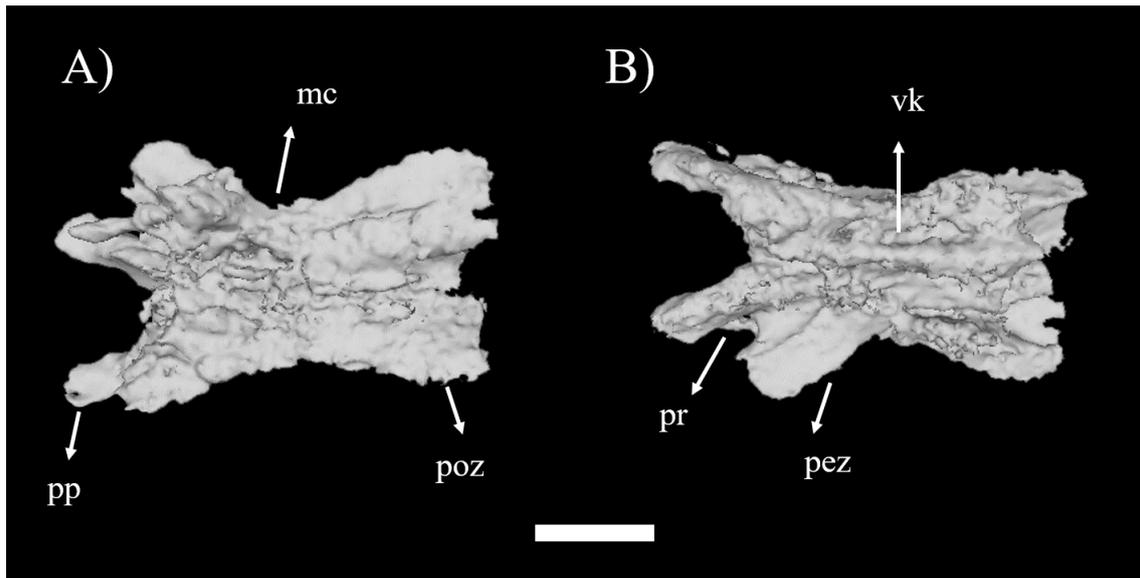


Figure 29: Isolated trunk vertebra in dorsal (A) and ventral (B) views. Abbreviations: mc: medial constriction; pez: prezygapophyses; poz: postzygapophyses; pp: parapophyses; pr: parasphenes. Scale bar = 1 mm.

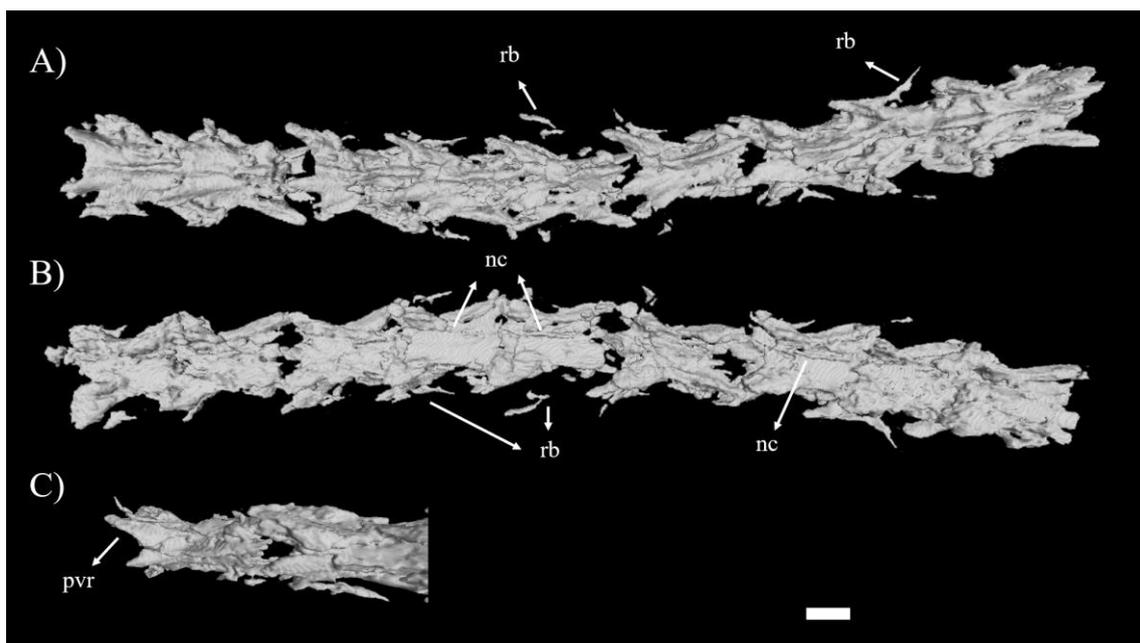


Figure 30: Sequence of 9 trunk vertebrae in ventral (A) and dorsal (B) views, and details of the sixth vertebra of this sequence in an oblique ventral view (C). Abbreviations: nc: nuchal crests; pvr: parasphenes' ventral ridge; rb: ribs. Scale bar = 1 mm.

6.4.4. Ribs

Due to the fragmented and compressed condition of the postcranium, the identification of the ribs (Figure 31) is especially difficult. Most of the cases it is not

possible to differentiate them from other fragments adjacent to the vertebrae. However, in some parts of the skeleton, isolated ribs are relatively well preserved.

The ribs are broad anteriorly, however they gradually narrower posteriorly. They are completely straight along their entire length, so there is no evidence of posterior flexion, even in ribs still articulated to the vertebrae. The capitulum is relatively elongated anteriorly compared to the tubercle, and in some, but not all ribs, this feature is particularly pronounced. The dorsal tips are thin and pointed.

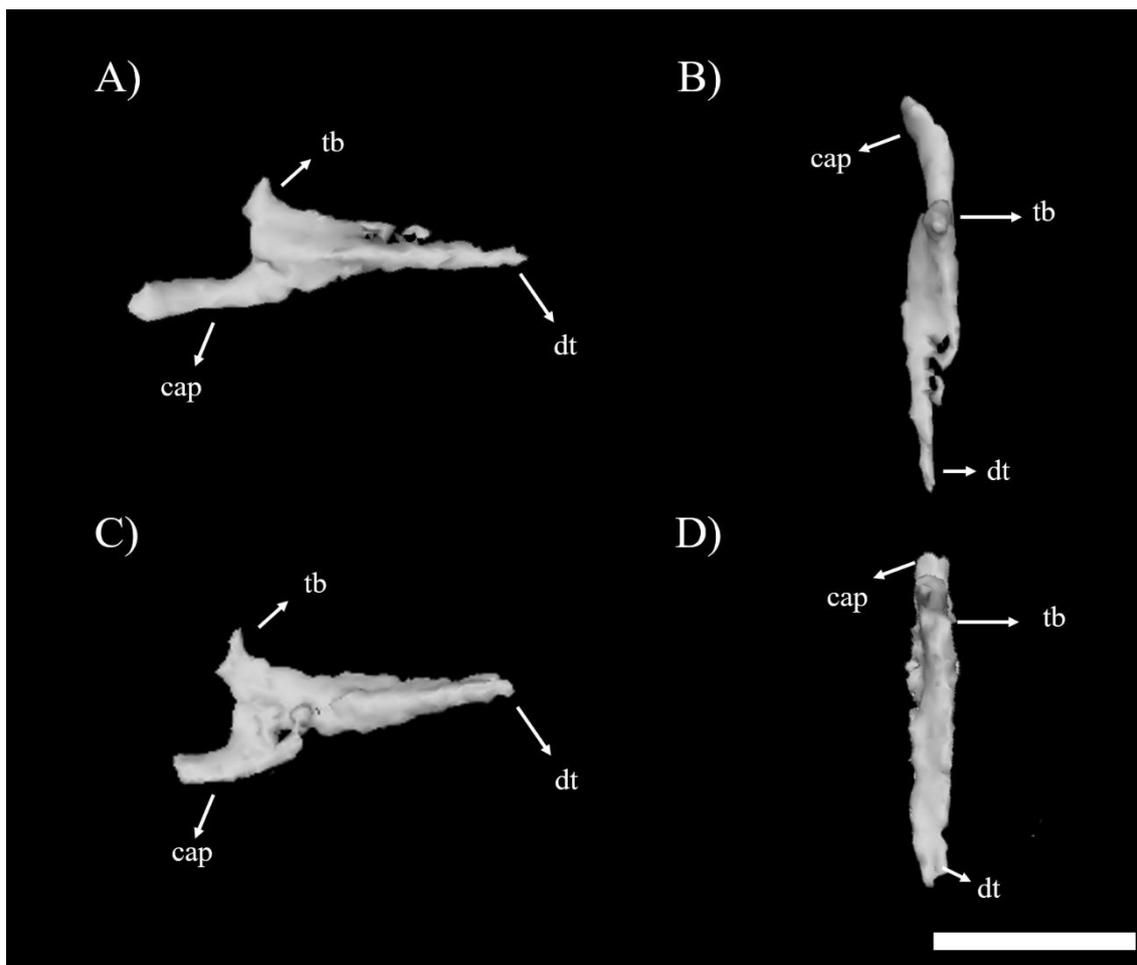


Figure 31: Ribs of DGM 1462-R in lateral (A) and dorsal (B) views. The rib figured in A-B comes from an anterior portion of the column (around 25th position), whereas the rib figured in C-D is associated with the vertebrae of figure 29 (around 40th position). Abbreviations: cap: capitulum; dt: distal tip; tb: tuberculum. Scale bar = 1 mm.

6.5. Phylogenetic analysis

A total of 66 most parsimonious trees (MPT's) with a length of 117 steps were recovered in the phylogenetic analysis using equal weighting. The best score was

achieved in 3433 out of 5000 replications. The values of consistency and retention indexes were 0.58 and 0.85, respectively. As usual in phylogenetic analyses of caecilians, rhinatrematids were chosen for rooting the tree (e.g. Wilkinson, 1992).

The strict consensus tree (Figure 32) recovered a monophyletic Teresomata and found DGM 1462-R nested within Typhlonectidae within a polyphyletic assemblage roughly equivalent to the Caeciliidae (see table 1 of Wilkinson *et al.*, 2011 for a brief summary of Caeciliidae classification history). Values of Bremer Supports, Standard Bootstrap, and Jackknife were plotted in the strict consensus trees (Figures 31, 32, and 33, respectively).

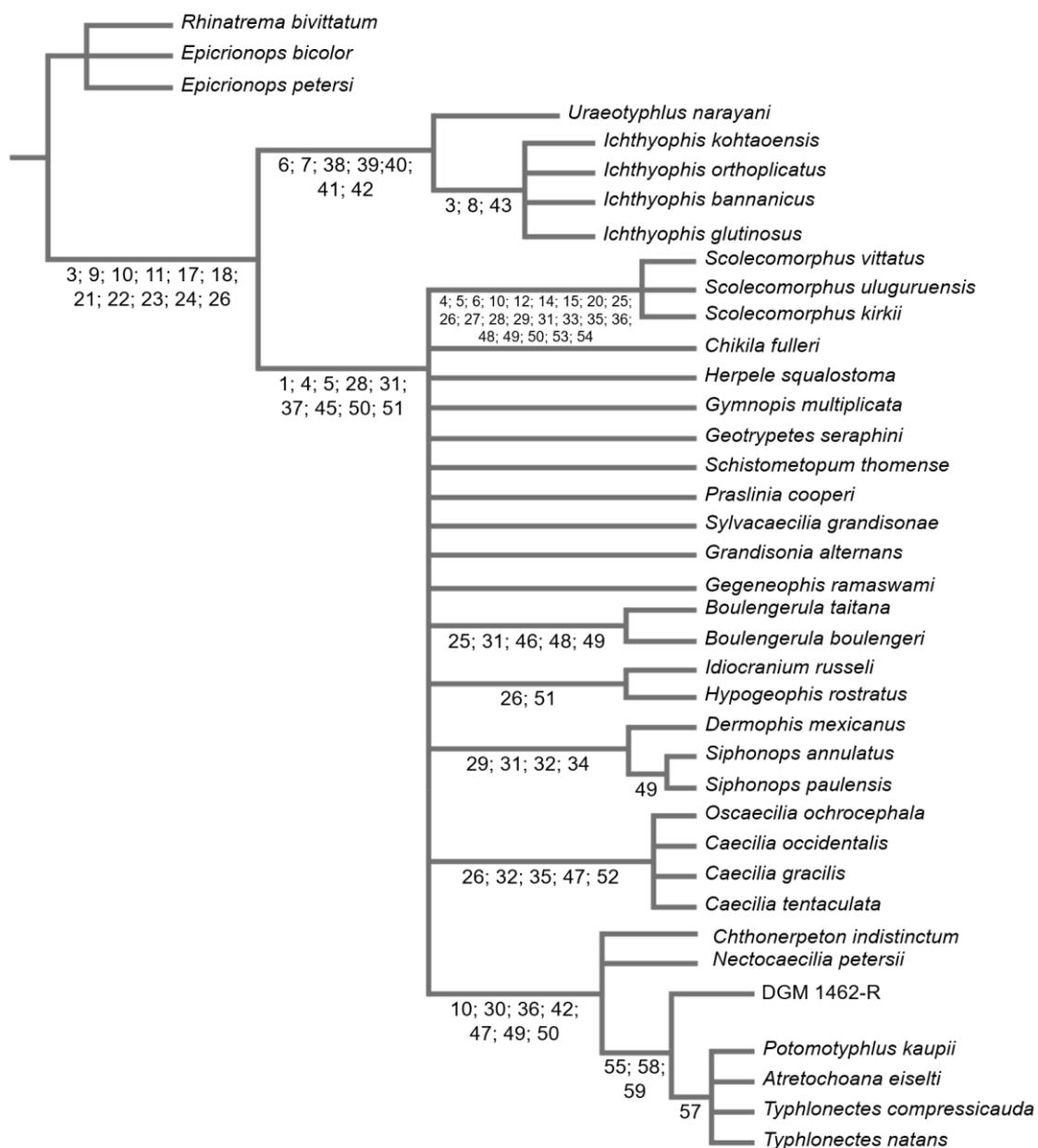


Figure 32: Strict consensus of 66 MPT's presenting the common synapomorphies supporting each branch.

Bremer supports (from 96941 trees, cut 0)

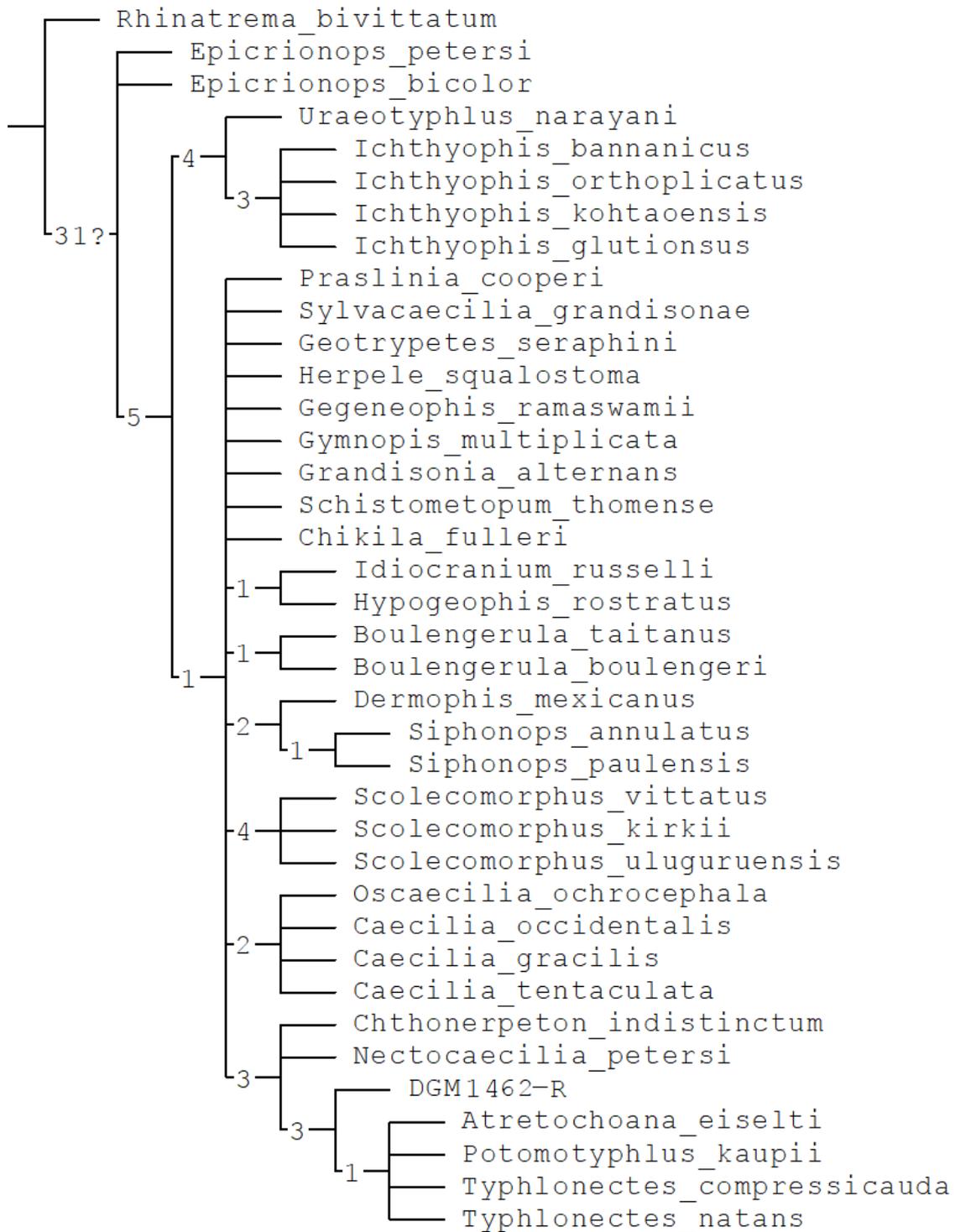


Figure 33: Values of Bremer Supports in the strict consensus tree.

GC values, 10000 replicates, cut=0 (tree 0) - Standard Bootstrap

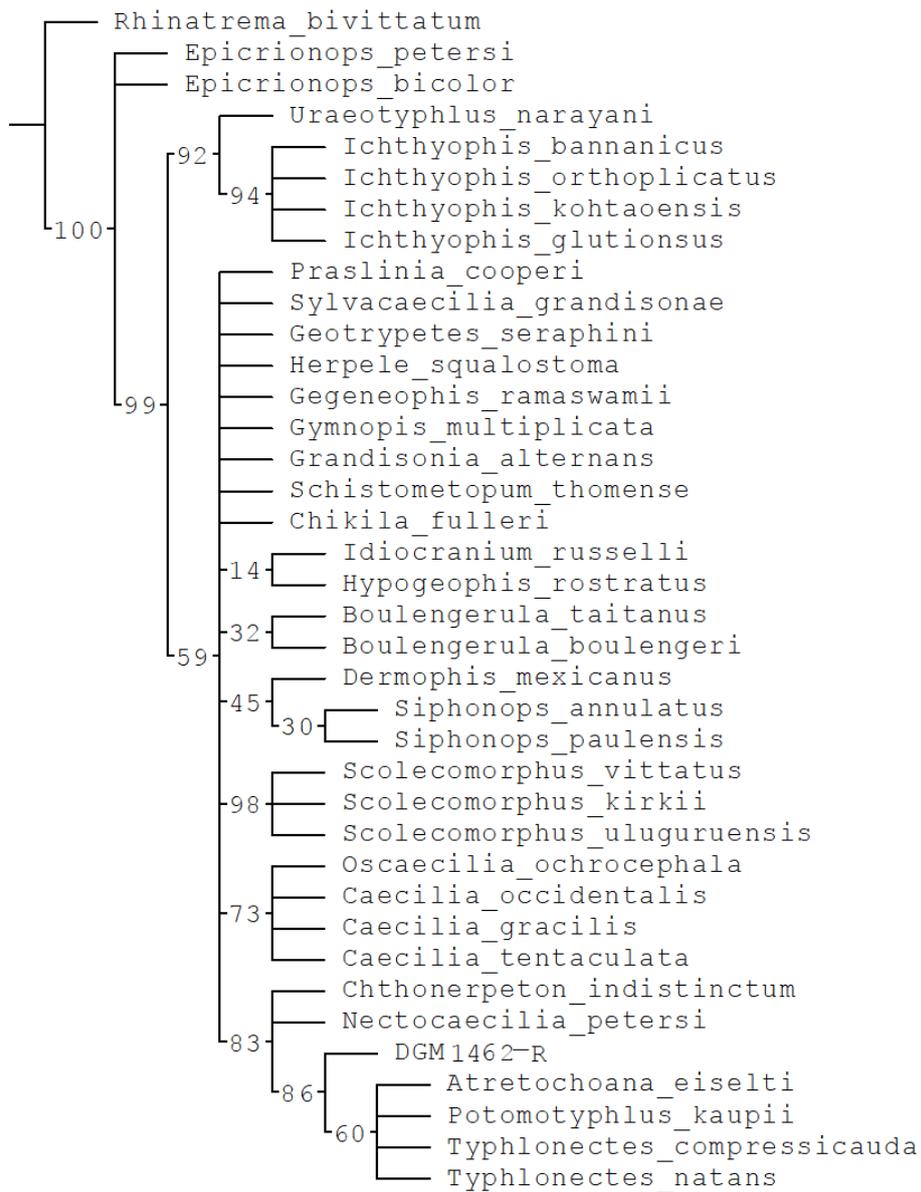


Figure 34: GC values of Standard Bootstrap in the strict consensus tree.

GC values, 10000 replicates, cut=0 (tree 0) - Jackknifing (P=36)

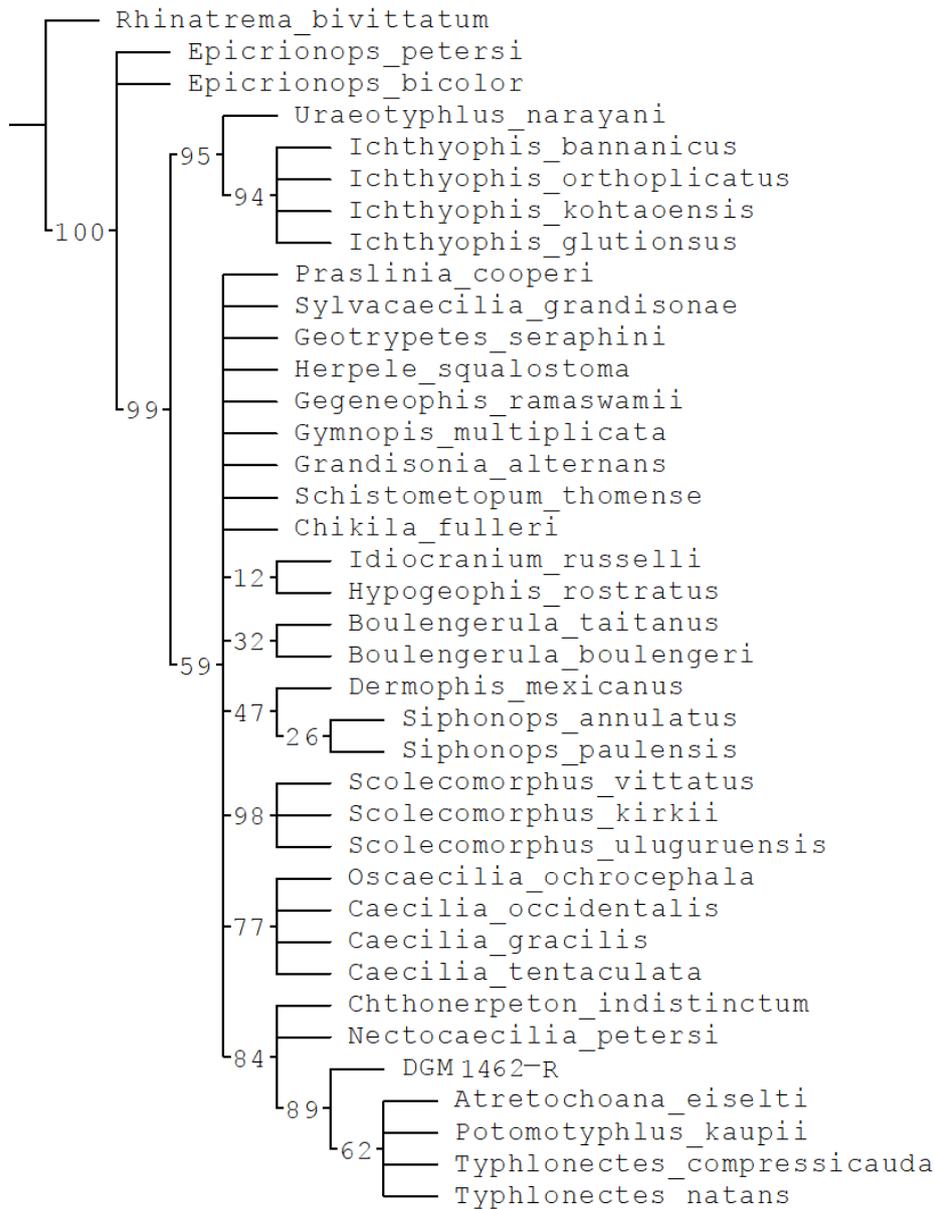


Figure 35: GC values of Jackknife in the strict consensus tree.

7. Discussion

The specimen DGM 1462-R shares a large number of unique features with caecilians, such as pseudangular, pseudodentary, os basale, absence of limbs and girdles, and vertebrae with amphicoelous centra, medially constricted, pronounced ventral keel and well-developed parasphenes (Wake, 1980; Wilkinson & Nussbaum, 2006). Therefore, its identification as a Gymnophiona is secure. Caecilian fossils are rare, usually restricted to isolated vertebrae and in this scenario, DGM 1462-R stands out, because it represents along with *Eocaecilia micropodia* the only caecilian fossils with preserved skull and postcranium still articulated (Jenkins & Walsh, 1993). Additionally, along with an anuran specimen described, but not yet named (Barcelos, 2016), they constitute the only two amphibians known for the Taubaté Basin.

7.1. Comparative anatomy

Among caecilians, there are two kinds of skull roof shape: opened dorsally, with temporal fenestrae present (zygokrotaphic), or closed and without such fenestrae (stegokrotaphic) (e.g. Kleinteich *et al.*, 2012). The presence of these fenestrae is directly related to the parietals, as these bones form the medial border of the upper temporal fenestra and serve as an anchoring surface for the adductor muscles (Nussbaum, 1983). In stegokrotaphic taxa, the parietals tend to be flat dorsal surfaces, without a pronounced ventral curvature (Figure 36. C), whereas in zygokrotaphic taxa, the parietals usually have strong ventral curvatures (Figure 36. A). However, there are exceptions to this general pattern. The stegokrotaphic *Dermophis mexicanus* has curved parietals (Figure 36. B), whereas the zygokrotaphic *Atretochoana eiselti* has completely flat parietals (Wilkinson & Nussbaum, 1997).

The shape of the skull roof in DGM 1462-R remains uncertain because although the parietals exhibit a slope (Figure 36. D), this feature is compatible either with stegokrotaphic as with zygokrotaphic skulls. In addition, there is no preserved squamosal among the skull fragments of DGM 1462-R, and therefore, the presence of an upper temporal fenestra could not be directly verified. Typhlonectids have a zygokrotaphic skulls, presumably secondarily (Taylor, 1968; Nussbaum, 1977, 1983), and the parietal slope is more prominent in *Chthonerpeton* and *Nectocaecilia*, less pronounced in *Typhlonectes* and *Potomotyphlus*, and absent in *Atretochoana* (Wilkinson & Nussbaum,

1997). The shape and proportions of the DGM 1462-R parietals are compatible with typhlonectids, especially *Chthonerpeton* and *Nectocaecilia*.

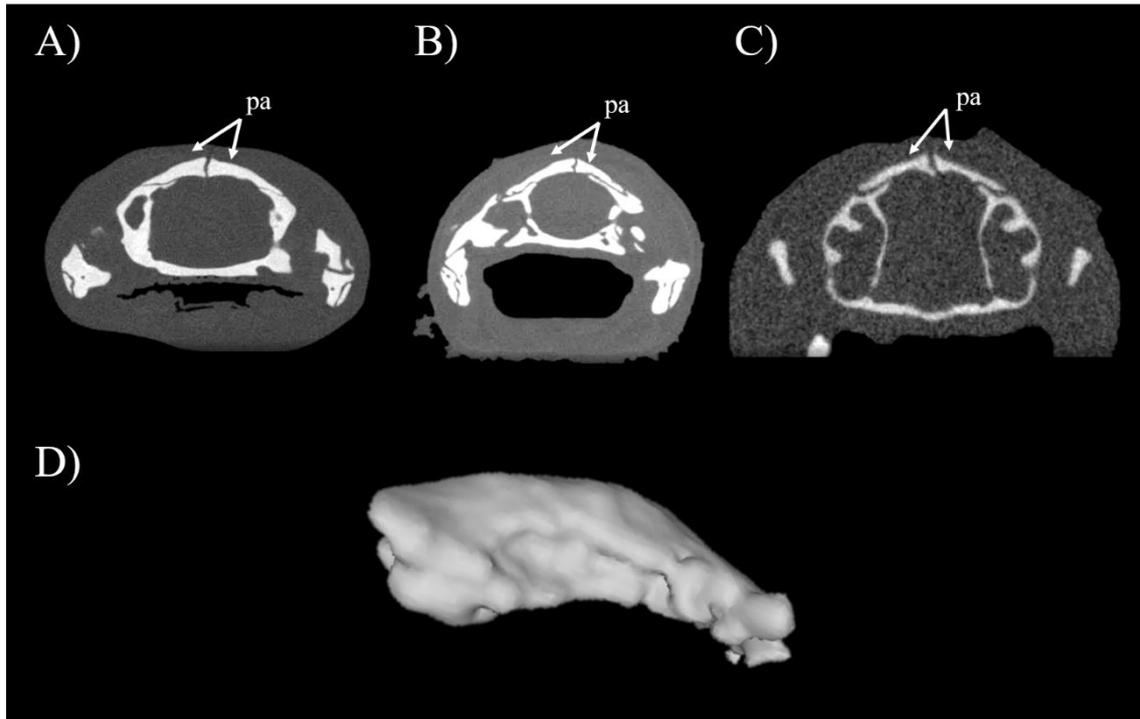


Figure 36: Coronal slices in anterior views of *Typhlonectes natans* (A), *Dermophis mexicanus* (B), and *Microcaecilia iwokramaie* (C) skulls. D) Parietal of DGM 1462-R in posterior view showing a slope. Abbreviations: pa: parietals. Figures not in scale. Data of slice images were obtained from Digimorph website (<http://digimorph.org>).

Gymnophionans have numerous foramina on the os basale lateral walls, including foramen ovalis, jugular foramen, and antotic foramina (Maddin *et al.*, 2012). In a fragment associated with the lateral portion of the basale of DGM 1462-R (Figure 25. B) there are 2 foramina whose precise identification is still uncertain, as two options are possible. The foramina could be interpreted as the foramen ovalis (anterior) and the jugular foramen (or only the jugular, as in some caecilians this foramen is divided into two small foramina), but also with the main antotic foramen (anterior) and the accessory foramen (posterior).

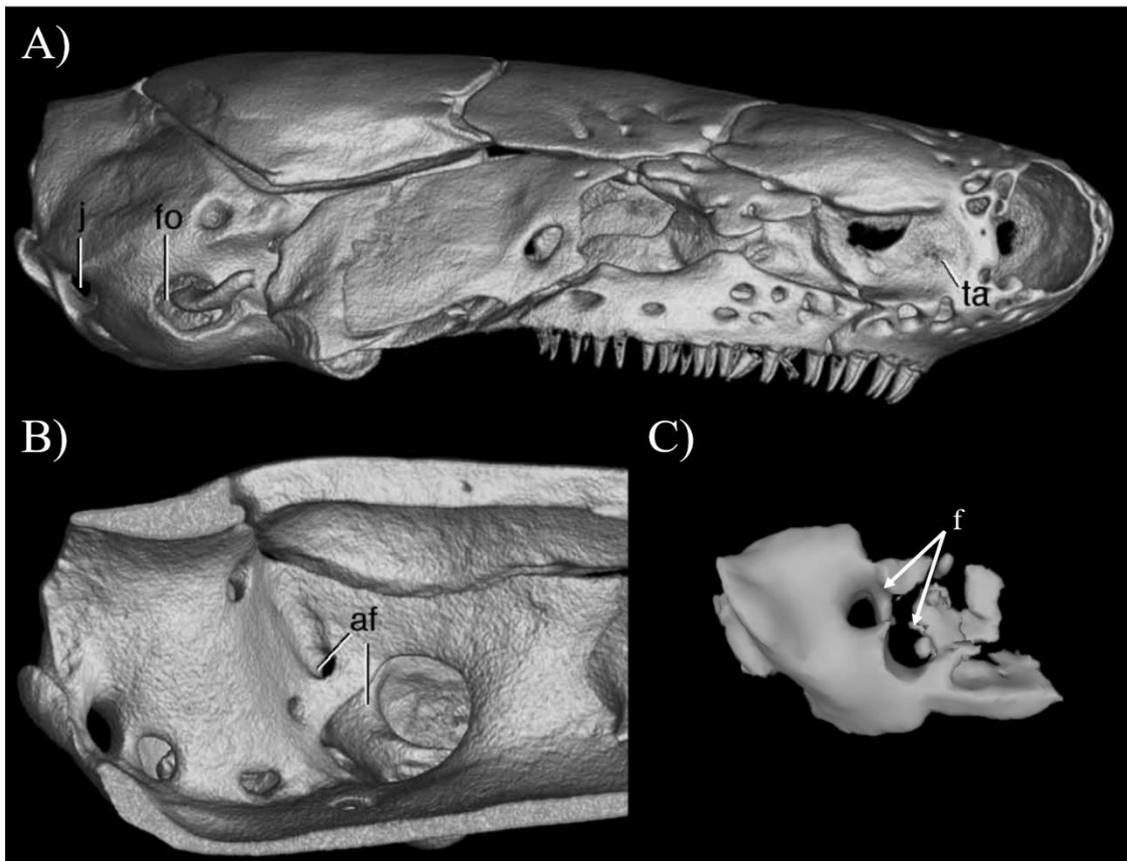


Figure 37: CT-scan of *Typhlonectes compressicauda* skull (A), with details of the antotic region (B). Lateral view (horizontally inverted to facilitate comparisons) of an os basale fragment of DGM 1462-R (C), showing two foramina. Abbreviations: af: antotic foramina; f: foramina; fo: foramen ovalis; j: jugular foramen; ta: tentacular aperture. Modified from Wilkinson *et al.* (2011). Figures not in scale.

In *T. compressicauda* (Figure 37. A), the foramen ovalis has an outline compatible with the anterior foramen of DGM 1462-R (Figure 37. C). However, the jugular foramen is located more posteriorly to it, not immediately posterodorsally as in the fossil specimen. In some typhlonectids, such as *Chthonerpeton*, *Potomotyphlus*, and *Atretochoana*, there is only a single antotic foramen, whereas in *Typhlonectes* (Figure 37. B) and *Nectocaecilia* an accessory foramen is also present (Wilkinson & Nussbaum, 1999; Maddin, 2011). Therefore, the anterior foramen could also be associated to the main antotic foramen, and the posterior one to the accessory foramen. However, unlike *Typhlonectes*, the accessory foramen would be located immediately posterodorsally to the main foramen.

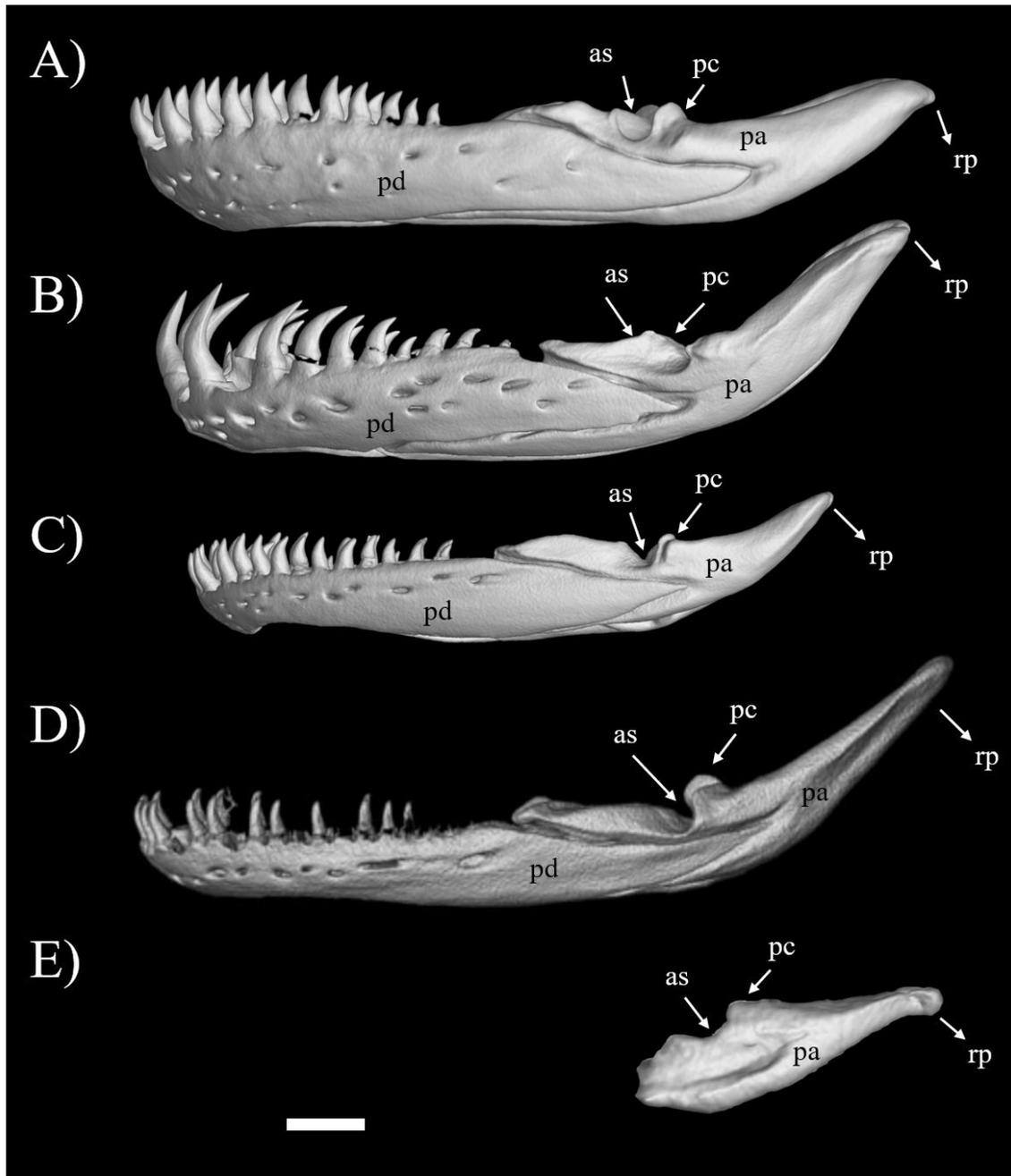


Figure 38: Caecilian lower jaws in lateral view. A) *Siphonops paulensis*. B) *Caecilia tentaculata*. C) *Chthonerpeton indistinctum*. D) *Typhlonectes compressicauda* (modified from Wilkinson *et al.*, 2011). E) DGM 1462-R. Abbreviations: as: articular surface; pa: pseudangular; pc: processus condyloides; pd: pseudodentary; rp: retroarticular process. Scale bar = 1 mm.

The gymnophionan lower jaw is formed by 2 elements: a posterior pseudangular and an anterior toothed pseudodentary (Wake & Hanken, 1982). Both bones are present in DGM 1462-R, although the pseudodontaries are fragmented and considerations about their anatomy remain difficult to be inferred. However, the left pseudangular is well

preserved, except for its anteriormost portion, presenting distinct characteristics typical of caecilians, such as the retroarticular and internal processes (Figure 26).

Unlike rhinatrematids (Nussbaum, 1977; 1983), the pseudangular is more robust and recurved. Regarding the size, among the compared taxa (Figure 38) the proportions are more similar to those of *Chthonerpeton*. Unlike *Siphonops* (Figure 38. A), a well-developed lateral crest is present but similar to it, the retroarticular process is projected posteriorly. Among typhlonectids, the retroarticular process is completely dorsally projected in *Atretochoana*, posterodorsally in *Potomotyphlus*, *Chthonerpeton* (Figure 38. C) and *T. compressicauda* (Figure 38.D), or posteriorly in *T. natans* (Wilkinson & Nussbaum, 1997; Wilkinson *et al.*, 2011). Therefore, the condition present in DGM 1462-R is similar to the latter.

Posteriorly to the pseudangular articular surface, the caecilians exhibit the processus condyloides. This process is usually well-developed and dorsally projected from the pseudangular dorsal surface (Figure 39. A-D). Unlike other caecilians, the processus condyloides in DGM 1462-R (Figure 26) is limited to a slight and dorsally oriented lift. Anteriorly to the articular surface, the caecilians bear the canalis primordialis (Figure 39), through which the mandibular nerve and artery pass. In all typhlonectids (e.g. Figure 39. C-D), except *Atretochoana*, the canalis primordialis is located just anteriorly to the articular surface (Wilkinson & Nussbaum, 1997). In DGM 1462-R, the region anterior to the articular surface is flat (Figure 39) and there are no signs of the presence of the canalis primordialis, which is probably located in an anteriormost pseudangular portion, that was not preserved in the fossil specimen.

Gymnophionans have bicuspid or monocuspid pedicellate teeth, arranged into two upper and two lower teeth rows (Wake, 1976). In some taxa, the inner mandibular tooth row could be absent (e.g. Wilkinson *et al.*, 2011). The total tooth count is also uncertain, but 21 isolated teeth were recognized. The semicircular and concentric outline of the upper tooth row is present in the skull (Figure 23. A-E, D-E), but the damaged and scattered condition of the specimen prevents the recognition and association of the isolated teeth to a specific series.

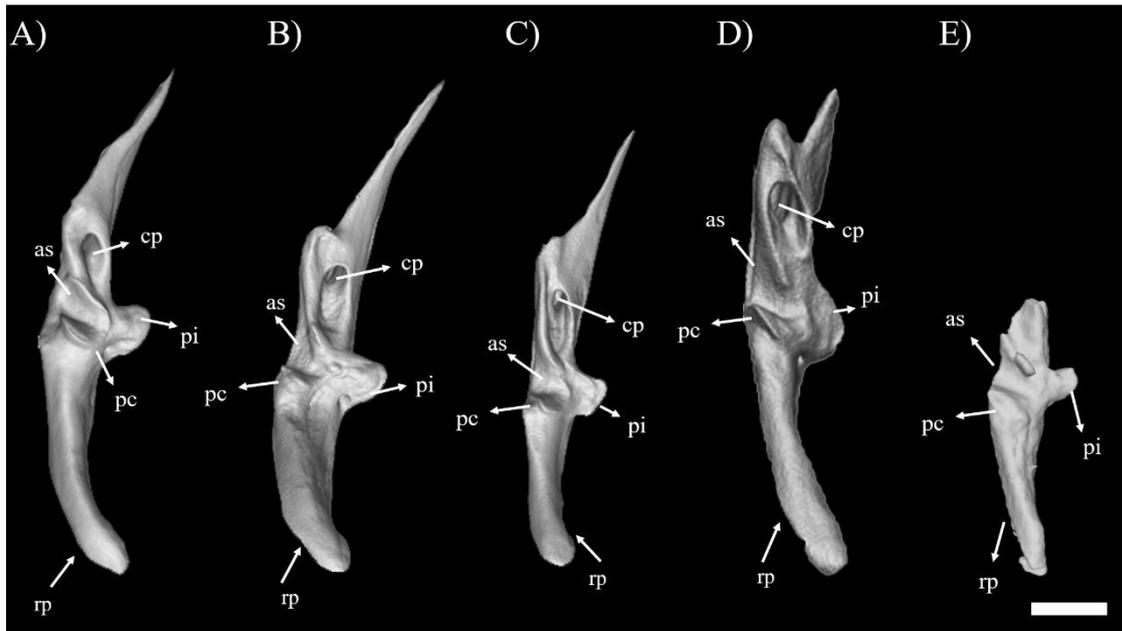


Figure 39: Caecilian pseudangulars in dorsal view. A) *Siphonops paulensis*. B) *Caecilia tentaculata*. C) *Chthonerpeton indistinctum*. D) *Typhlonectes compressicauda* (modified from Wilkinson *et al.*, 2011). E) DGM 1462-R. Abbreviations: as: articular surface; cp: canalis primordialis; pa: pseudangular; pc: processus condyloides; pi: processus internus; rp: retroarticular process. Scale bar = 1 mm.

Considering adult typhlonectids, the teeth have only a single cusp, are conical and anteroposteriorly curved, and bear lateral flanges (Wilkinson, 1991). However, *T. compressicauda* differs from this pattern and has a chisel-shaped tooth (Greven, 1986). The tooth morphology of DGM 1462-R (Figure 23. D-E) is compatible with Typhlonectidae, as all teeth are monocusped, conical, curved, and with a pointed apex. The presence of blade-shaped side flanges is uncertain, due to the size of these structures.

According to Taylor (1977), anterior vertebrae of caecilians, especially the atlas and the second vertebra, are taxonomically informative. However, Wilkinson *et al.* (2011) point out that the lack of knowledge about the morphological variety of caecilian vertebrae difficult the use of these structures for taxonomic purposes. The entire postcranial region is present in DGM 1462-R, including the atlas and the second vertebra, although both are damaged.

The vertebral count is inaccurate, as the posterior region of the body was not preserved and some vertebrae present are highly fragmented, so their individualization is complicated. However, approximately 62 vertebrae were recognized. Considering the missing portions of the vertebral sequence, and the shape of the most posterior vertebrae of the specimen, approximately half to $\frac{3}{4}$ of the specimen total body length was preserved.

Considering other typhlonectids, the vertebral count ranges from 81-88 in *Chthonerpeton* to 141-143 in *Nectocaecilia* (for more details see Table 2 in Wilkinson & Nussbaum, 1997).

The atlas present in DGM 1462-R is incomplete but preserves structures that allow recognizing similarities with living species. As in *Chthonerpeton* (Figure 40. C2), in lateral view, the atlantal cotyles are flat and inclined anteroposteriorly. In anterior view, the cotyles are fused, unlike the condition of *Siphonops* and *Caecilia* (Figure 40. A2 and B2, respectively), but similar to the morphology observed in *Chthonerpeton* (Figure 40. C2), differing only in the presence of a more pronounced medial notch. The atlas centrum in DGM 1462-R does not have a ventral keel, which is also absent in *Siphonops* and *Caecilia* (Figure 40. A3 and B3, respectively).

Regarding its neural arch, only the bases of the anterior margins and the portions anterior to the postzygapophyses remain preserved. Among typhlonectids, only in *Chthonerpeton* (Figure 40. C4) and *Nectocaecilia* these anterior projections on the margins are fused. As in the fully aquatic typhlonectids, in *Siphonops* (Figure 40. A4) and *Caecilia* (Figure 40. B4), the projections in DGM 1462-R (Figure 40. D4) remain separate. According to Wilkinson & Nussbaum (1997), the pronounced constriction anterior to the postzygapophyses, present in DGM 1462-R (Figure 27.A) is a distinctive characteristic of fully aquatic taxa, being absent in semi-aquatic typhlonectids (e.g. Figure 40. C5) and the remaining caecilians (e.g. Figure 40. A5-B5).

As the second vertebra present in DGM 1462-R is highly fragmented, morphological comparisons are difficult. The prezygapophyses are wide, and the centrum has a ventral keel, as in *Chthonerpeton*, *Siphonops*, and *Caecilia*. In all of these taxa, the second vertebrae bear ribs, but the presence of these elements in the second vertebra of DGM 1462-R is uncertain since such structures were not identified.

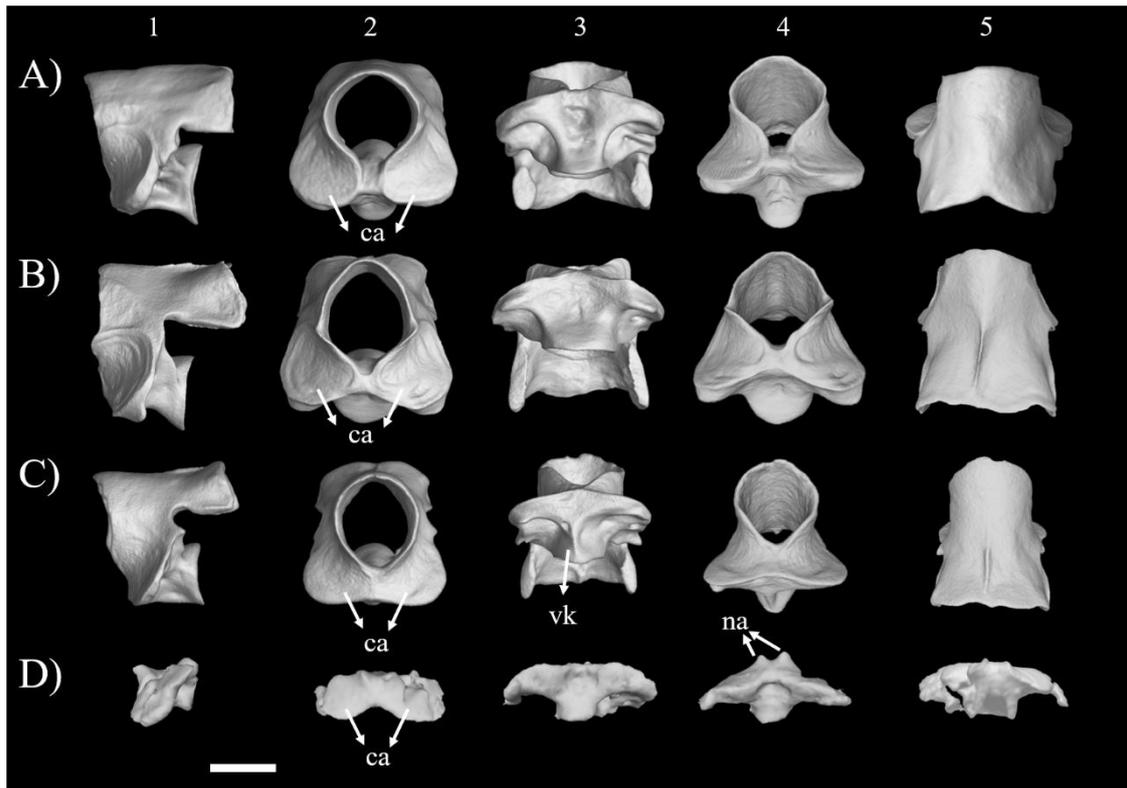


Figure 40: Caecilian atlases in lateral (column 1), anterior (column 2), ventral (column 3), oblique ventral (column 4), and dorsal (column 5) views. A) *Siphonops paulensis*. B) *Caecilia tentaculata*. C) *Chthonerpeton indistinctum*. D) DGM 1462-R. Abbreviations: ca: cotyles of atlas; na: neural arches; vk: ventral keel. Scale bar = 1 mm.

The morphology of the most posterior trunk vertebrae (Figure 41) is typical of caecilians, including the presence of structures such as the amphicoelous centrum constricted medially and presenting a well-developed ventral keel, parasphenes projecting anteriorly, flat neural arches with nuchal crests (e.g. Taylor, 1977; Wake, 1980, Wilkinson & Nussbaum, 1997). Among typhlonectids, strong nuchal crests are characteristic of *Chthonerpeton* and *Nectocaecilia*, whereas in the other taxa they are poorly developed or even absent in posterior trunk vertebrae (e.g. Wake, 1980; Azpelicuelta *et al.*, 1987; Wilkinson & Nussbaum, 1999). Elongated and narrow vertebrae characterize the typhlonectids with aquatic habits, whereas broad and short vertebrae, similar to other non-typhlonectid caecilians are characteristic of the semi-aquatic *Chthonerpeton* and *Nectocaecilia* (Wilkinson & Nussbaum, 1999).

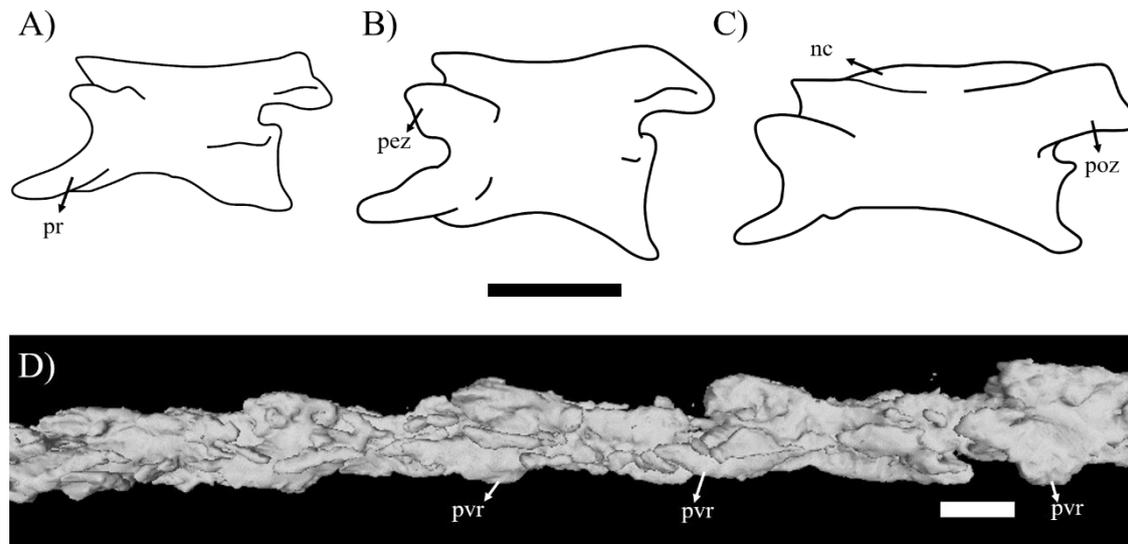


Figure 41: Caecilian trunk vertebrae in lateral view. A) Redrawn of *Ichthyophis glutinosus* vertebra from Wake (1980). B) Redrawn of *Dermophis mexicanus* vertebra from Wake (1980). C) Redrawn of *Chthonerpeton indistinctum* vertebra from Azpelicueta *et al.* (1987). D) Vertebral sequence of DGM 1462-R. Abbreviations: nc: nuchal keel; pez: prezygapophyses; poz: postzygapophyses; pr: parasphenes; pvr: parasphene ventral ridge. Scale bars = 1 mm.

The elongation of trunk vertebrae is present in the specimen DGM 1462-R (note the low values of the width/length ratio in Table 1, comparing mainly to *T. natans* and *T. compressicauda*), roughly similar to *Typhlonectes*. Another characteristic feature of the trunk vertebrae in DGM 1462-R is the highly developed ventral ridge on the parasphenes. This feature is common to all typhlonectids, except *Chthonerpeton* (Wilkinson & Nussbaum, 1999) but it seems to be especially conspicuous in the vertebrae of DGM 1462-R.

Several ribs are present in the vertebral column of the specimen DGM 1462-R however they are usually damaged and difficult to identify. Two of them, located on the anterior and the middle portions of the specimen, remain fully preserved. The ribs have a straight outline and are dorsoventrally expanded at their anterior portion, but narrows distally and exhibit pointed distal tips. The capitulum is elongated anteriorly. Considering typhlonectids, an elongated capitulum is present only in *Typhlonectes natans*, and the ribs are broad throughout the trunk in *Chthonerpeton*, *Nectocaecilia*, *Atretochoana*, and *Potomotyphlus*, but are posteriorly narrow in *Typhlonectes* (Wilkinson & Nussbaum, 1997). The ribs in *Chthonerpeton* (Figure 42. B; E), *Nectocaecilia*, and other caecilians are straight, similar to the pattern observed in DGM 1462-R, but in aquatic typhlonectids

the ribs show a strong posterior flexure, curving them posteriorly (Wilkinson & Nussbaum, 1999).

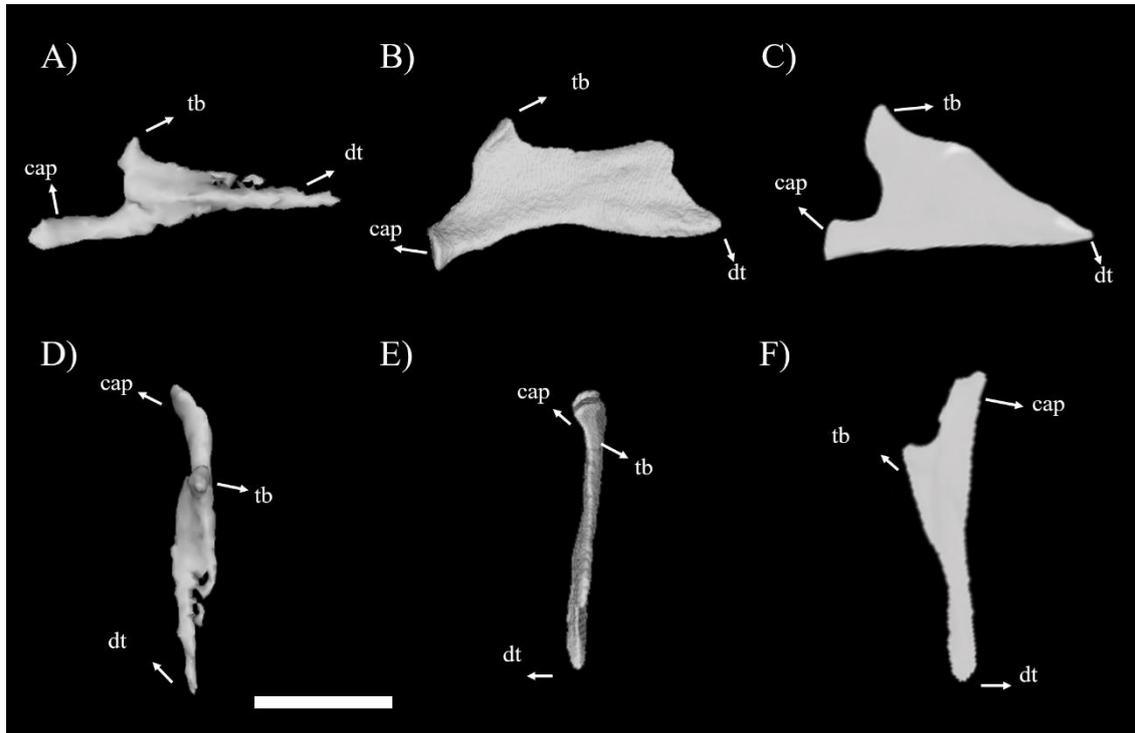


Figure 42: Caecilian ribs in lateral (A, B, and C) and dorsal (D, E, and F) views. Rib of DGM 1462-R in lateral (A) and dorsal (D) views. A rib of *Chthonerpeton indistinctum* in lateral (B) and dorsal (E) views. A rib of *Typhlonectes natans* in lateral (C) and dorsal (F) views (modified from Digimorph website). Abbreviations: cap: capitulum; dt: distal tip; tb: tuberculum. Scale bar = 1 mm.

Therefore, as shown above, the DGM 1462-R specimen has several features typically associated to Typhlonectidae, such as the elongation of the vertebrae, the presence of pronounced constrictions anterior to the postzygapophyses on atlas, and well-developed ventral ridges on the parasphenes of trunk vertebrae. Indeed, all the morphological characteristics of the specimen are congruent with at least one of the taxa that comprise this family. Even characteristics whose correct identification is still uncertain, such as the presence of upper temporal fenestrae or the identity of the foramina on the os basale lateral walls, have interpretations compatible with the morphology of typhlonectids.

7.2. Phylogenetic affinities

Due to the incompleteness of the DGM 1362-R specimen, only 10 of the 60 characters (16.6%) used in this analysis could be scored. The presence of taxa whose

scoring is based on incomplete specimens can potentially lead to a decrease in accuracy in the results of phylogenetic analyses (e.g. Wilkinson, 1995; Anderson, 2001). However, as shown by Wiens (2003), the problem itself is not the amount of missing data, but the lack of diagnostic characters that possibilities to recognize the relationships between taxa. DGM 1462-R shares several features unique to typhlonectids, which are considered to be derived among caecilians, and therefore its phylogenetic positioning is well-supported.

In the strict consensus tree obtained from 66 MTP's (In the original analysis by Wilkinson, 1997, using a similar but not equal dataset, 23 MPT's were obtained), 7 of the 10 currently known families (Kamei *et al.*, 2012) of gymnophionans were recovered as monophyletic (despite Chikilidae was represented by only one species in this analysis), with the exception of Herpelidae, Indotyphlidae, and Dermophiidae. Indeed, the recovered topology is roughly similar to the most recent results using molecular data (e.g. San Mauro *et al.*, 2014), but with a lower resolution among Teresomata. The DGM 1462-R specimen is nested within a monophyletic Typhlonectidae, which is placed in a large polytomous clade, with a content approximately equivalent to Caeciliidae sensu Frost *et al.* (2006).

Phylogenetic relationships among "caeciliids" constitute a major problem in the phylogeny of gymnophionans. For a long time, all described caecilians were included within Caeciliidae, and thus this clade became a heterogeneous assemblage with numerous taxa (Taylor, 1968; Wilkinson & Nussbaum, 2006; Wilkinson *et al.*, 2011). Even with the widespread use of molecular data and the improvement in the classification, in which "Caeciliidae" was subdivided into monophyletic families, such as Chikilidae, Herpelidae, Indotyphlidae, Siphonopidae and Dermophiidae (e.g. Wilkinson *et al.*, 2011; Kamei *et al.*, 2012), the "Caeciliidae" paraphyly problem remains but now restricted to the genus level.

Considering Typhlonectidae, the topology of the strict consensus tree has similarities with the results of previous phylogenetic analyses (Figure 43), using both morphological and molecular data (Wilkinson & Nussbaum, 1999; Maciel *et al.*, 2016). In all of them, the clade formed by the fully aquatic typhlonectids (*Typhlonectes*, *Potomotyphlus*, and *Atretochoana*) is the sister group of *Chthonerpeton* and *Nectocaecilia*, both with semi-aquatic habits. However, the relationships between the species that comprise each of these subgroups are less resolved. The DGM 1462-R specimen occupies an intermediate position among typhlonectids, congruent with its

morphology, as it exhibits a combination of derived characters of taxa adapted to aquatic environments along with features considered plesiomorphic among typhlonectids.

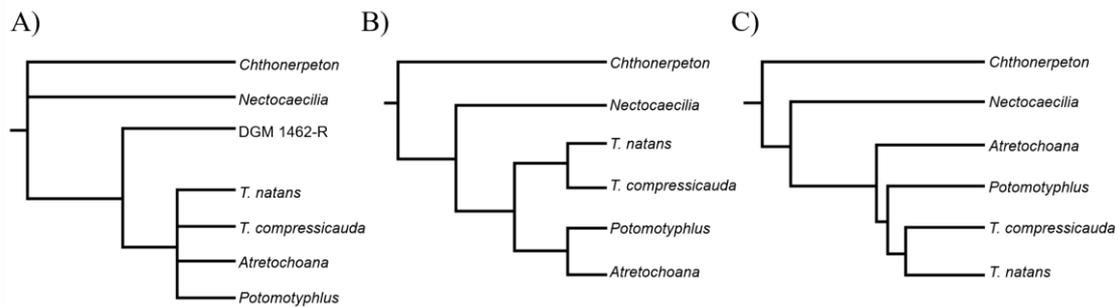


Figure 43: Different proposals for the phylogenetic relationships among typhlonectids. A) Topology recovered in this work. B) Topology from Wilkinson & Nussbaum, 1999, using morphological data. C) Topology recovered by Maciel *et al.*, 2016 using morphological and molecular data.

The value of the total consistency index (CI) is relatively low (0.58). In the original analysis, with fewer taxa and less 8 characters, Wilkinson (1997) found CI = 0.64. The relatively low value may be related to the large number of homoplastic characters present in the analysis, especially among the poorly resolved “Caeciliidae”. The values for the retention index (0.85) are relatively high and were also equal in both analyses, which means that the data is informative.

The highest support values of Bremer (Figure 33), Bootstrap (Figure 34), and Jackknife (Figure 35) are present in clades traditionally recognized as monophyletic in analyses with different data sources (e.g. Maddin *et al.*, 2012b; San Mauro *et al.*, 2014), such as Neocaecilia, Ichthyophiidae, and Scolecomorphidae. Among teresomatans, the values are generally low, but in Typhlonectidae and in the branch formed by DGM 1462-R + the fully aquatic typhlonectids, the values are considerably higher.

The analysis using Implied Weighting (IW, $k = 3.0$) showed a higher resolution in its topology when compared to the results of the analysis with Equal Weighting (EW), and also less MPT’s (1 in IW, 66 in EW). When compared to the more recent topologies of Gymnophiona (e.g. Kamei *et al.*, 2012; San Mauro *et al.*, 2014), the resulting tree (Figure 44) also recovers Scolecomorphidae as a sister group of the remaining “caeciliids”, in addition to Caeciliidae sensu Wilkinson *et al.* 2011 as a sister group of Typhlonectidae, whereas both of them were nested in a large polytomy in the EW analysis.

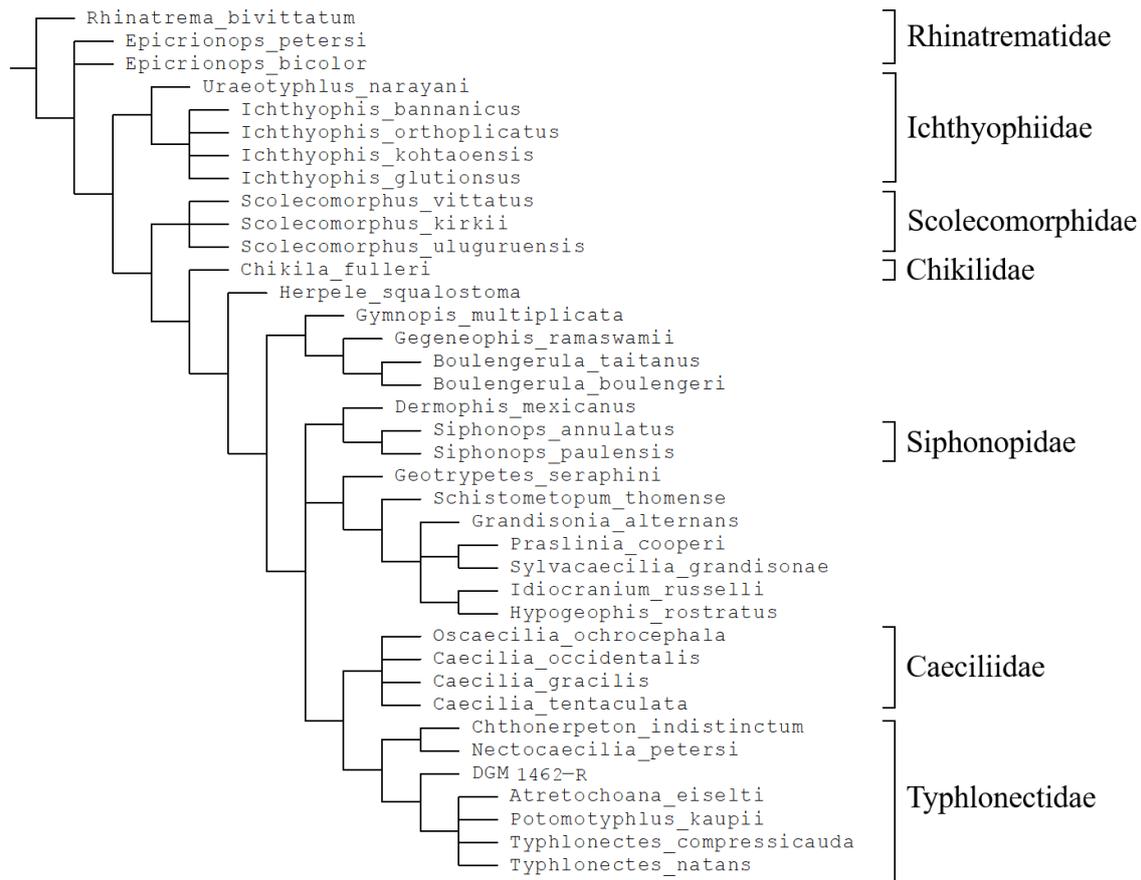


Figure 44: Topology recovered using IW (k=3.0).

The phylogenetic relationship between DGM 1462-R and the others typhlonectids still needs to be better evaluated, preferably in an analysis focused only in them. Due to its particular morphology, combining features of aquatic and semi-aquatic typhlonectids, the specimen DGM 1462-R is particularly important to understand the evolution of Typhlonectidae.

7.3. Taphonomical considerations

Since during the moment of material collection, the standard procedures related to obtaining taphonomic data (such as the definition of the azimuthal orientation or the top and the bottom of the fossiliferous assemblage) were not followed, taphonomic interpretations are naturally limited (Holz & Simões, 2002). Indeed, the DGM 1462-R specimen was originally treated as mining tailings and stored along with other similar materials exposed to weathering until finally being collected.

Barcelos (2016) described a fossil anuran also from Tremembé Formation, and assigned it to Microhylidae, based on a damaged and disarticulated specimen. According to him the disarticulation and fragmentation of the material could be related to ‘bloat and float’ stage. During this stage, after the death the unburied carcass decay due to endogenous bacteria, in a process that generates gases and allows the carcass, when located in aquatic environments, to remain floating until a rupture in the skin followed by the escape of these gases appears (e.g. Syme & Salisbury, 2014).

Members of Typhlonectidae differ from other caecilians by presenting aquatic or semi-aquatic habits. Among typhlocentids, *Chthonerpeton* seems to be the less adapted to the aquatic environment, being usually found in wet soil areas but also swimming in small ponds (Taylor, 1968; Tanner, 1971; Gudynas *et al.*, 1988). *Nectocaecilia* lack some morphological adaptations related to the aquatic lifestyle (e.g. fins), however it has already been observed occupying muddy burrows in banks of streams and also between roots of floating vegetation (Gorzula and Señaris 1998; Maciel & Hoogmoed, 2011), whereas the other typhlonectids are considered to be fully adapted to an aquatic existence (e.g. Wilkinson & Nussbaum, 1997).

Although fragmented, the specimen DGM 1462-R is still articulated, except for skull and the middle portion of the fossil, in which scattered and isolated elements are found. A possible interpretation of this condition is that a scavenger reworked only a part of the carcass, which remained articulated due to the absence or low intensity of transport between the death and the deposition, while the fragmentation and compression of the remains could be explained by the compaction from the sediment layers.

Lacustrine environments have low energy available for the transport of the remains, and their bottom is generally poor in oxygen (e.g. Wetzel, 1983), factors that contribute to the fossilization and were present in the Tremembé palaeolake (Riccomini, 1989; Chagas *et al.*, 2009). The phylogenetic positioning of the DGM 1462-R specimen, nested with taxa known for their aquatic or semi-aquatic lifestyles, is another evidence corroborating the taphonomic interpretation proposed.

7.4. Implications for the Time Range of Caecilians

The caecilian fossil record is sparse and scattered through time (Figure 45). Regarding Cenozoic deposits, the record comprises poorly preserved specimens assigned

only to *Gymnophiona* indet. (see more details in the section 4). Considering this scenario, DGM 1462-R represents the first caecilian known for Oligocene deposits, filling a gap of ~30 Ma between *Apodops* and the Napak XV skull.

The Eocene-Oligocene transition was a key moment in the history of the Earth, marked by the extinction of several groups and the beginning of the global cooling period, mainly in high latitudes places (Coxall & Pearson, 2007), despite little is known about the impacts on the caecilian evolutionary past, with few exceptions. For example, Kamei *et al.* (2013) noted that the divergence between the species comprising Chikilidae occurred > 25 Ma, although they still retain many external similarities.

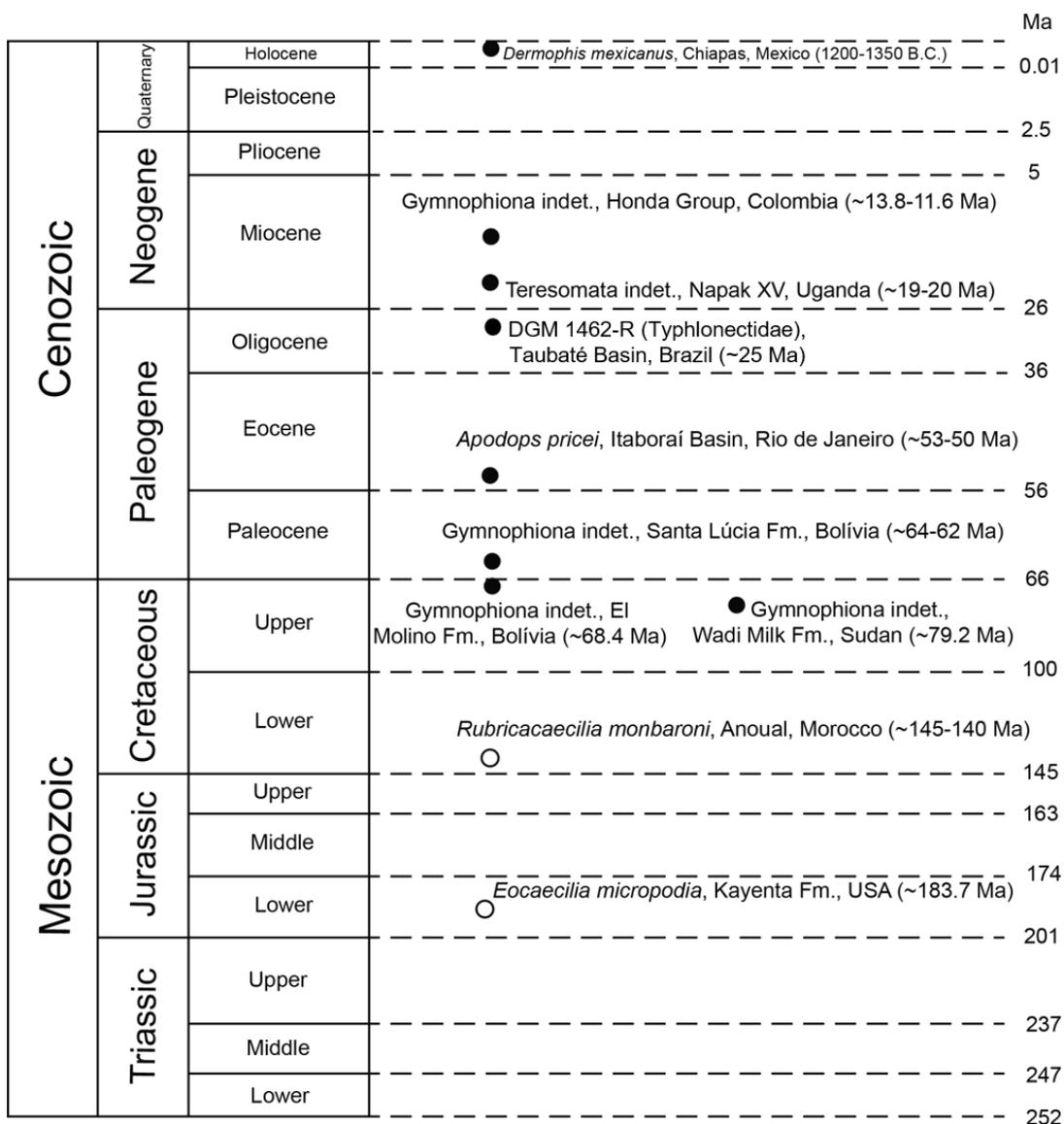


Figure 45: Distribution of the fossils assigned to Gymnophionomorpha through geological time, including the record of DGM 1462-R. Solid black circles indicate crown-group taxa, whereas circles with a black outline and white filling indicate stem-lineages.

According to Maciel (2016, chapter 5), it was also during this period that the divergence between a part of the fully aquatic typhlonectids occurred (except *Atretochoana*, whose divergence with the other lineages occurred earlier, during the middle Eocene). Therefore, the presence of a different typhlonectid lineage further south during the Oligocene suggests that the group experienced an even greater diversity than the previous works considered.

7.5. Biogeography of Typhlonectidae

Biogeographical aspects of most caecilians are unknown, with some exceptions (e.g. Gower *et al.*, 2002; Loader *et al.*, 2007; Zhang & Wake, 2009). The group has distribution typically Gondwanan (Hedges *et al.*, 1993), but the patterns for most taxa do not appear to follow the sequence of landmass breakup followed by vicariance events (Kamei *et al.*, 2012). Maciel (2016, chapter 5) discussed the biogeographic history of typhlonectids. According to their analysis, the group emerged in the northern portion of South America, approximately 85 Ma ago, and *Chthonerpeton* dispersed towards southernmost regions of the continent, while the distribution of fully aquatic typhlonectids remains limited to the northern basins.



Figure 46: Distribution of modern caecilians, with the fossil occurrences marked, including DGM 1462-R (number 10 in this map). For more details see the Figure 14. Modified from Cogger & Zweifel (1998) and Loader *et al.* (2007).

In this scenario, the presence of another lineage of typhlonectids in the southern regions of America (Figure 46) may represent a separate dispersion event for the group. The contact between the northern and Paraná basins persisted until approximately 30 Ma (Lundberg *et al.*, 1998), and the Taubaté Basin is located next to the Tietê River basin, a tributary of the upper Paraná river (Malabarba, 1998). Age estimates for Tremembé Formation Basin associate this unit to Chattian, ~25 Ma (Lima *et al.*, 1985), thus allowing dispersion to occur. However, this remains just a plausible conjecture, and tests are required to corroborate, or not, this hypothesis.

8. Conclusions

Gymnophiona remains a poorly-known clade in many aspects of its evolutionary past. Its fossil record, when compared to that of other lissamphibian groups, especially anurans, is particularly scarce, and therefore the description of new specimens assigned to the group could contribute significantly to advances in the understanding of the caecilian biology.

A review of the caecilian fossil record, along with a detailed description and phylogenetic positioning of the DGM 1462-R specimen was presented. The compilation of information about taxa known only by fossils and assigned to caecilians allows recognize and discuss patterns on their record trough space and time. The morphological comparison between fossil and living caecilians showed how the study of fossils can directly impact the knowledge of modern groups.

According to these analyses, the specimen is closely related to typhlonectids, especially fully aquatic taxa. The main evidence for this close relationship comes from the postcranial morphology, in features such as the elongation of the trunk vertebrae, constriction anterior to the postzygapophysis on atlas, and the presence of ventral ridges on the parasphenes.

The results obtained here represent the first attempt to include a fossil of a crown caecilian in a phylogenetic analysis containing living taxa. Therefore, the DGM1462-R specimen is the first caecilian based on fossil material ever assigned to a family containing modern taxa. It also represents the first occurrence for the group in the Oligocene, and is the second known lissamphibian found in the Tremembé Formation.

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10. Appendix

10.1. Character list

1. True tail (postcloacal vertebrae and annuli): present (0) or absent (1). T1 in Wilkinson (1997);
2. Tertiary annuli: absent (0) or present (1). T2 in Wilkinson (1997);
3. Positioning of the mouth: (0) terminal, slightly subterminal (1), strongly subterminal (2). T3 in Wilkinson (1997);
4. Fusion between nasals and premaxillae: (0) absent or present (1). T4 in Wilkinson (1997);
5. Septomaxillae: present (0) or absent (1). T5 in Wilkinson (1997);
6. Prefrontals: present (0) or absent (1). T6 in Wilkinson (1997);
7. Postfrontals: present (0) or absent (1). T7 in Wilkinson (1997);
8. Contact between frontals and squamosal: present (0) or absent (1). T8 in Wilkinson (1997);
9. Contact between squamosal notch with the os basale process: absent (0), or present (1). T9 in Wilkinson (1997);
10. Skull roof: Opened (*Zygokrotaphic*), in which the *m. mandibulae externus* pass-through temporal fossa and meet at the skull dorsal midline (0), closed, also known as *Stegokrotaphic* (1), and opened (*Zygokrotaphic*) but with the adductor muscles not reaching the dorsal midline of the skull (2). T10 in Wilkinson (1997);
11. Parasphenoid: parallel sided (0) or converging anteriorly (1). T13 in Wilkinson (1997);
12. Orbitosphenoid shape: vertical (0) or oblique (1). T14 in Wilkinson (1997);
13. Separation of Maxillopalatine and Quadrate: (0) separated by a large pterygoid, by a small pterygoid and the pterygoid process of quadrate (1) or only by the pterygoid process (2). T15a in Wilkinson (1997);
14. Expansion of Mediopalatinal canal: present (1) or absent (0). T15b in Wilkinson (1997);
15. Basipterygoid process: absent (0), weakly developed (1) well developed (2). T16 in Wilkinson (1997);
16. Stapes morphology: perforated (0) or imperforate (1). T17 in Wilkinson (1997);

17. Lateral contact between Quadrate and Maxillopalatine: present (0) or absent (1). T18 in Wilkinson (1997);
18. Shape of the Retroarticular process: short and straight (0) or long and recurved (1). T19 in Wilkinson (1997);
19. Morphology of the posterior glossal skeleton: ceratobranchial 4 absent (0), ceratobranchials 3 and 4 fused and little expanded (1) or ceratobranchials 3 and 4 fused and much expanded (2). T20a in Wilkinson (1997);
20. Larynx enclosed by the fused Ceratobranchials 3 and 4: absent (0) or present (1). T20b in Wilkinson (1997);
21. Insertion of anterior fibres of m. interhyoideus anterior on ceratohyal: (0) present or absent (1). T22 in Wilkinson (1997);
22. Number of bundles of M. interhyoideus posterior: (0) one or two (1). T24 in Wilkinson (1997);
23. Positioning of M. interhyoideus posterior: predominantly oblique (0) or predominantly horizontal (1). T25 in Wilkinson (1997);
24. Positioning of M. depressor mandibulae: predominantly vertical (0), or predominantly longitudinal (1). T27 in Wilkinson (1997);
25. Orbit condition: open (0) or covered by bone (1). T28 in Wilkinson (1997);
26. Positioning of tentacular aperture: adjacent to eye (0), between eye and naris (1), or beneath naris (2). T29 in Wilkinson (1997);
27. Phallodeum morphology: aspinous (0) or spinous (1). T30 in Wilkinson (1997);
28. Vent morphology: longitudinal (0), or transverse (1) or circular (2). T31 in Wilkinson (1997);
29. Splenial teeth: present (0) or absent (1). T32 in Wilkinson (1997);
30. Size of choanal openings: small (0) or large (1). T33 in Wilkinson (1997);
31. Narial plugs: absent (0) or present (1). T35 in Wilkinson (1997);
32. Skull roof morphology: with Mesethmoid covered dorsally (0) or exposed between the frontals (1). T36 in Wilkinson (1997);
33. Diastema in prevomerine teeth: absent (0) or present (1). T38 in Wilkinson (1997);
34. Maxillopalatine completely surrounding the Choane: absent (0) or present (1). T39 in Wilkinson (1997);
35. Size of some or all premaxillary-maxillary teeth: small (0) or all enlarged (1). T40 in Wilkinson (1997);

36. Mode of reproduction: Oviparous (0) or viviparous (1). T42 in Wilkinson (1997);
37. Type of development: with a larval stage (0) or direct (1). T43 in Wilkinson (1997);
38. External division of atria: (0) absent or present (1). T44 in Wilkinson (1997);
39. Shape of anterior pericardial space: short and small (0) or long and extensive (1). T45 in Wilkinson (1997);
40. Number of posterior internal flexures in m. rectus laterals: less than two (0) or two (1). T46 in Wilkinson (1997);
41. Number of internal flexures on m. subvertebralis: zero (0) or one (1). T47 in Wilkinson (1997);
42. Tracheal lung: absent (0) or present (1). T48 in Wilkinson (1997);
43. Morphology of anterior annuli: orthoplicate (0) or angulate (1). T49 in Wilkinson (1997);
44. Contact between m. rectus laterals: meeting mid-dorsally (0) or absent (1). T50 in Wilkinson (1997);
45. Anterior internal flexures in m. rectus lateralis: present (0) or absent (1). T51 in Wilkinson (1997);
46. Development degree of Myosepta in m. obliquus externus superficialis: well developed (0), dorsal only (1), or absent (2). T52 in Wilkinson (1997);
47. Origin of ventral part of m. subvertebralis: from the midcentrum (0), or subvertebralis (1). T53 in Wilkinson (1997);
48. Terminal keel on body termini: absent (0), or present (1). T54 in Wilkinson (1997);
49. Annular scales, secondary annuli and segmented body termini: present (0) or absent (1). T55 in Wilkinson (1997);
50. Shape of m. interhyoideus posterior: short (0), or elongate (1). T56 in Wilkinson (1997);
51. Anterior dentary teeth morphology: (0) bicuspid or monocuspid (1). T57 in Wilkinson (1997);
52. Shape of vomeropalatine tooth rows: forming a semicircle (0), or an angle (1). T58 in Wilkinson (1997);
53. Stapes: absent (0) or present (1). A1 in Wilkinson (1997);
54. Internal process of Pseudangular: absent (0) or present (1);

Scolecormorphus_vittatus

102000110211?11?11211111121010001011100000001001101000000??

Chikila_fulleri

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Typhlonectes_compressicauda

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Nectocaecilia_petersi

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Chthonerpeton_indistinctum

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Potomotyphlus_kaupii

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Atretochoana_eiselti

10211111021?20211120110101020110?00??0000001??0101011111110

Schistometopum_thomense

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Siphonops_paulensis

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Siphonops_annulatus

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Caecilia_tentaculata

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Caecilia_gracilis

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Caecilia_occidentalis

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Osaecilia_ochrocephala

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Hypogeophis_rostratus

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Grandisonia_alternans

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Dermophis_mexicanus

102111110110202111201111010210010101100000001000011011000000

Gymnopsis_multiplicata

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Gegeneophis_ramaswamii

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Herpele_squalostoma

10201110011?102011?0111?110?0011?0001000000????00110110000??

Boulengerula_boulengeri

102111110110202?11201111110?100100001000000111011110110000??

Boulengerula_taitanus

102111110110202011201111110?000000001000000111011110110000??

Geotrypetes_seraphini

102111110210202111201111020?001100011000000010000100110000?0

Sylvacaecilia_grandisonae

102111110110202111201111010?0010000000??00????00100110000??

Idiocranium_russelli

102111110110202111201111020?00100000100??00????00100110000??

Praslinia_cooperi

10211110011??01111?0111?000?0000?0000000000????001?0110000??

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????????????????1????????????0????????????????10?11?0110

11. Biography

Academic Degree: Bachelor in Biological Sciences by the Universidade Federal de Uberlândia (UFU), Uberlândia, Minas Gerais, Brazil.

Monography: Análise das macro e microestruturas presentes em dentes de Theropoda e Baurusuchidae da Bacia Bauru

Published paper:

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