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Pseudosuchia: Masters of survival and diversification

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Q18	AUTHOR: Please provide the "volume number" for reference Woodward, Aubier, Sena & Cubo, 2024.	

INTRODUCTION

Pseudosuchia: Masters of survival and diversification

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Abstract

In the context of an increasing interest for Pseudosuchia, we have compiled a Special Issue, comprising 14 collaborative studies that deepen our understanding of pseudosuchian evolution. These contributions range from the description of a new taxon to exhaustive reviews of thermometabolism, morphological adaptation, systematics, and detailed investigations into ontogeny, paleoneurology, paleohistology, and paleobiology. Through these papers, we explore the evolutionary history of pseudosuchian archosaurs, spotlighting their rise and diversification following the end-Permian mass extinction.

KEYWORDS

Archosauria, paleobiology, phylogeny, pseudosuchian

1 | INTRODUCTION

It is with great pleasure that we introduce this special issue of *The Anatomical Record*, which showcases a collection of research on the systematics and paleobiology of pseudosuchians. After the keen interest in dinosaurs that followed the publication of Crichton's book (1991) and Spielberg's film (1993) on *Jurassic Park*, paleontologists became increasingly interested in closely related groups, particularly Pseudosuchia. This issue is, thus, timely, and follows the influential "The Dawn of an Era: Comparative and Functional Anatomy of Triassic Tetrapods" recently published in the journal (Pinheiro et al., 2024). This earlier issue reported significant advances in understanding the paleobiology of pseudosuchians (among other taxa), with a focus on the Triassic period in South America.

The rapid divergence of the Pseudosuchian clade, occurring less than 10 million years after the appearance of the earliest archosaurs, led to a wide array of body forms and adaptations (Nesbitt et al., 2010). By the Late Triassic, pseudosuchians had diversified, ranging from quadrupedal and bipedal terrestrial locomotion to

semiaquatic and pelagic lifestyles (Brusatte et al., 2008; Foth et al., 2016), and dietary habits comprising piscivory, carnivory, omnivory, and even herbivory (e.g., Gauthier et al., 2011; Nesbitt et al., 2013).

Pseudosuchia are archosaurs, including taxa more closely related to Crocodylia than to Avemetatarsalia (or Ornithodira, a group that includes pterosaurs, silesaurids, and dinosaurs, including birds) (Nesbitt, 2011). This issue aims to serve as a keystone for current research, enhancing our comprehension of these fascinating archosaurs and their roles in present and past ecosystems.

According to Parker et al. (2021), Pseudosuchia comprises several distinct groups: Ornithosuchidae, Erpetosuchidae, Aetosauria, Gracilisuchidae, and Loricata. Ornithosuchidae, Erpetosuchidae, and Aetosauria form a basal group, and the latter two were retrieved more closely related to each other. Loricata (sensu Nesbitt, 2011) includes the "rauisuchians" and the Crocodylomorpha. Notably, all groups except Crocodylomorpha became extinct by the end of the Triassic period, as reported by Nesbitt (2011) and Toljagic and Butler (2013). "Rauisuchians" were large terrestrial

1 predators with osteoderms, known during the Triassic,
2 encompassing all suchian taxa outside of Aetosauria or
3 Crocodylomorpha (sensu Nesbitt et al., 2013). This par-
4 ticular group was a characteristic component of most
5 Triassic land ecosystems (Gower, 2000). Crocodylomor-
6 pha, the only group of recent pseudosuchian archos-
7 saurs that survive the Triassic-Jurassic extinction
8 (Benton & Clark, 1988; Clark et al., 2001; Nesbitt,
9 2011), evolved in the Late Triassic. Through the Meso-
10 zoic and Cenozoic, they diversified into various groups,
11 from small, terrestrial omnivores and large predators
12 to herbivores and highly adapted aquatic and marine
13 forms. This diversification is related to the develop-
14 ment of an akinetic skull and the capacity for strong
15 biting forces in modern crocodylians, marking a
16 critical evolutionary transition (Erickson et al., 2012;
17 Langston, 1973; Leardi et al., 2020). The basal crocody-
18 lomorphs, often referred to as sphenosuchians, are
19 recorded in Upper Triassic and Lower Jurassic sedi-
20 ments across North and South America, Eurasia, and
21 Africa (Clark et al., 2001), showcasing their early suc-
22 cess as small, cursorial predators.

23 Ornithosuchidae has been found in different phyloge-
24 netic positions across Archosauria (e.g., Ezcurra, 2016;
25 Nesbitt, 2011; Sereno, 1991). However, the most of hypothe-
26 ses after Sereno (1991) converged on a position near the
27 base of Pseudosuchia. All members of this group are carniv-
28 orous, putatively scavengers, and facultatively bipedal dur-
29 ing fast gaits (von Baczko et al., 2018; von Baczko &
30 Ezcurra, 2013). Nevertheless, the fossil record of the group
31 is geographically limited, with the description of a new
32 ornithosuchid, *Dynamosuchus collisensis*, from the Upper
33 Triassic sediments of Brazil (Müller et al., 2020).

34 The aetosaurus, known for their extensive and robust
35 dermal shield covering their bodies, represent another sig-
36 nificant group of terrestrial pseudosuchians (Parker &
37 Martz, 2011; Scheyer et al., 2014). These animals possessed
38 stout forelimbs and triangular skulls with unique dental
39 and cranial features, thriving during the Upper Triassic
40 across all landmasses but Antarctica and Australia (Desojo
41 et al., 2013; Reyes et al., 2020). While traditionally consid-
42 ered herbivores, recent studies suggest that aetosaurus
43 might have had a broader dietary spectrum (Desojo
44 et al., 2013; Reyes et al., 2024; Taborda et al., 2021).

45 Erpetosuchidae was proposed by Watson (1917) to
46 include *Erpetosuchus granti* from the Lossiemouth Sand-
47 stone Formation (late Carnian–Norian/Late Triassic),
48 Scotland, which recognized its relationship within Archos-
49 auria, possibly closer to phytosaurs and aetosaurus, but
50 also displaying some similarities to crocodylomorphs
51 (Benton & Walker, 2002). Current phylogenetic analyses
52 position Erpetosuchidae close to Ornithosuchidae (Müller
53 et al., 2020; von Baczko & Desojo, 2016).

Turfanosuchus dabanensis, from the Middle Triassic 54
of China, is the oldest known member of the Gracilisuchidae, 55
and underscores the expansive distribution of 56
early archosaurs across Pangaea from the latter part 57
of the Early Triassic onward. Initially, these archosaurs 58
may have been uncommon participants of the ecological 59
communities (Butler et al., 2014; Young, 1973). 60

61 Throughout the late Middle to early Late Triassic, gra-
62 cilisuchids exhibited a wide geographic reach, marking
63 their presence in the Tongchuan Formation in China and
64 the Chañares Formation in Argentina, situated at
65 roughly equivalent paleolatitudes in both hemispheres
66 (Lecuona et al., 2020; Wu & Russell, 2001; Young, 1973).
67 Most recently the first unambiguous gracilisuchid from
68 Brazil was described, *Parvosuchus aurelioi* (Müller, 2024).
69 The gracilisuchid fossil record is sparse, being repre-
70 sented by small-sized carnivorous forms, having a lack of
71 the distribution across Pangaea during the Triassic.

72 This introduction thus sets the stage for a detailed
73 exploration of the systematic relationships, paleobiologi-
74 cal, and biomechanical features of pseudosuchians within
75 the studies included in this special issue, highlighting
76 their ecological roles and their evolutionary histories.
77 These papers are grouped by topic and overviewed below.

2 | BIOMECHANICS

81 Ornithosuchids are characterized by an array of features
82 (e.g., the femur has a well-developed lesser trochanter) that
83 led some paleontologists to consider them as the origin of
84 theropod dinosaurs (Walker et al., 1964). We have known
85 since Gauthier (1986) that they are pseudosuchian archos-
86 saurs. von Baczko et al. (2024) performed a whole-body bio-
87 mechanical modeling of *Riojasuchus tenuisiceps*. They
88 discovered that this taxon was characterized by a roughly
89 erect (adducted) posture and a parasagittal gait with a plan-
90 tigrade pes. However, elucidating putative bipedalism in
91 *Riojasuchus* remains elusive using the data and methods
92 available. The authors questioned why these taxa became
93 extinct while bipedalism was an advantage for early dino-
94 saurs. They state that finding fossil trackway data is key for
95 answering the question of bipedalism.

3 | ONTOGENY

96 Farias et al. (2024) osteohistologically analyzed the ontoge-
97 ny of *Prestosuchus chiniquensis* from the Middle–Late
98 Triassic of Brazil and proposed a growth model for non-
99 crocodylomorph loricatans. Although Pseudosuchia are
100 classically assumed to have lower growth rates than Ave-
101 metatarsalia, these authors inferred high bone growth
102
103
104
105
106

1 rates in the youngest ontogenetic state. They were able to
2 characterize and describe six ontogenetic classes, from
3 early ontogeny (age class I; a state based on the analysis
4 of a humerus of *Decuriasuchus quartacolonina*), passing
5 through the acquisition of sexual maturity (age class IV),
6 to skeletal maturity (age classes V and VI). They showed
7 that the presence of an external fundamental system
8 (EFS) in *Prestosuchus* suggests that determinate growth
9 may be plesiomorphic in non-crocodylomorph loricatans.
10 Clarifying the taxonomic status of specimen
11 MCN-PV-10.105b assigned to *D. quartacolonina* is a
12 basic step necessary to draw solid conclusions about
13 the growth of non-crocodylomorph loricatans.

14 Parker et al. (2024) provide new insights into the mor-
15 phology, body size, and ecological role of the aetosaur
16 *Coahomasuchus kahleorum* through the study of a new
17 small-bodied specimen (TMM 31100-437) from the Late
18 Triassic Colorado City Formation of the Dockum Group
19 of Texas. Their analysis reveals that this species, previ-
20 ously thought to be characterized by autapomorphic lat-
21 eral osteoderms, possesses osteoderms with distinct
22 lateral and medial flanges and a dorsal eminence. Bone
23 histological data indicate that TMM 31100-437 was near
24 or at skeletal maturity at a body length of approximately
25 1.5 meters, indicating the presence of small-bodied taxa
26 within the armored pseudosuchians, Aetosauria. It also
27 demonstrates that small individuals could be interpreted
28 as adults, rather than an early ontogenetic stage of a large
29 sized species. Additionally, the dentition of small-bodied
30 *Coahomasuchus* indicates a diet potentially based on
31 scavenging or hunting small tetrapods and invertebrates,
32 similar to juvenile crocodylians.

33 Additionally, Johnson et al. (2024) examined the bone
34 histology of *Macrospondylus bollensis*, a teleosauroid from
35 the Early Jurassic of Germany, across different individuals
36 of differing body sizes. This study strongly suggested a con-
37 sistent growth rate during ontogeny, with attributed juve-
38 niles displaying woven and parallel-fibered bone tissue with
39 limited remodeling, and mature individuals showing
40 parallel-fibered bone tissue with lines of arrested growth
41 (LAGs) and an EFS formation in the outermost cortex. The
42 presence of unusual growth of disorganized bone tissue in
43 the cross-section of two specimens suggests a potential bone
44 disease. They concluded from the bone compactness that
45 *M. bollensis* is more like that of living crocodylians, support-
46 ing a coastal rather than pelagic lifestyle.

48 4 | PALEOBIOLOGY

49 Regarding the paleophysiology of pseudosuchians, Faure-
50 Brac (2024) provided an updated review of the evolution
51 of their thermophysiology, addressing endothermy in

52 more basal forms. This review summarized evidence on 54
53 thermometabolic strategies among different extinct taxa, 55
56 using quantitative histology and isotopic geochemistry 57
58 techniques. The author suggested that the loss of endo- 59
60 thermery in crocodylomorphs may be associated with the 61
62 end-Triassic mass extinction (ETME), which acted as a 63
64 physiological filter favoring the survival of slow-growing 65
66 ectothermic groups afterward (Faure-Brac, 2024). 67

68 Heck and Woodward (2024) tried to find proxies for 69
70 sex identification in extinct Pseudosuchia. As egg shell 71
72 formation requires a large amount of reserve calcium, 73
74 calcium metabolism may be a priori a powerful proxy for 75
76 this purpose. We know that birds utilize medullary bone 77
78 as a calcium reserve for egg-shelling. Heck and Wood- 79
80 ward (2024) hypothesized that crocodylians may mobilize 81
82 calcium ions from cortical bone and/or osteoderms, and 83
84 tried to use this process for sex identification purposes in 85
86 extinct Pseudosuchia. They analyzed undecalcified mid- 87
88 diaphyseal *Alligator mississippiensis* femoral bone cross- 89
90 sections and searched for cortical signals of reproduction 91
92 (i.e., evidence for resorptive processes linked to calcium 93
94 mobilization) but failed to find them. They concluded 95
96 that increasing the sample size and inclusion of speci- 97
98 mens with known reproductive histories may be neces- 99
100 sary for a more robust test of their hypothesis.

101 While many studies address the physiology of extinct 102
103 taxa by focusing on specific characteristics, Cubo et al. 104
105 (2024) emphasize an organismic approach to the ques- 106
107 tion. In this volume, the authors demonstrate their meth- 108
109 odology using femoral CT scans and thin-section 110
111 histology of the Early Jurassic metriorhynchoid *Pelago- 112
113 saurus typus*. The results were considered after applying 114
115 phylogenetic comparative methods. Bone compactness 116
117 values suggest an amphibious lifestyle, and the presence 118
119 of osteoderms with highly developed ornamentation indi- 120
121 cates periods of basking for thermoregulation. By esti- 122
123 mating the resting metabolic rate and red blood cell size, 124
125 they found *Pelagosaurus* to have an ectothermic thermo- 126
127 metabolism. Lastly, by exploring the maximum metabolic 128
129 rate and aerobic scope, Cubo et al. (2024) found that *Pela- 130
131 gosaurus* most likely employed sit-and-wait ambush tac- 132
133 tics or slow sustained subundulatory swimming, and 134
135 captured prey like the Gharial, using rapid lateral move- 136
137 ments of the head.

138 Woodward et al. (2024) propose a novel method to 139
140 retrodict the body mass of non-crocodylian pseudosu- 141
142 chians, based on a regression model using femur volume. 143
144 The authors suggest that this volumetric approach 145
146 reduces measurement errors and provides a more accu- 147
148 rate proxy for body mass estimation compared to tradi- 149
150 tional linear models. Their study, which is based on 151
152 *A. mississippiensis* body mass, was tested across individ- 153
154 uals from various crocodyliiform taxa. In large femora, 155

1 they observed discrepancies exceeding 100 kg between
2 body mass estimates derived from femur length and those
3 predicted by femur volume. Notably, the femur length-
4 based models tended to overestimate body mass in larger
5 specimens. Consequently, the authors advise caution
6 when using femur length as a predictor for retrodicting
7 the body mass of large extinct pseudosuchians, as it may
8 lead to inflated results. In contrast, femur volume
9 appears less sensitive to proportional limb differences
10 and may serve as a more reliable predictor of body mass
11 for extinct pseudosuchians.

14 | 5 | PHYLOGENY

15
16 Some included contributions explored one of the most
17 iconic groups of pseudosuchians, the Crocodylomorpha.
18 This group has generated much debate regarding its evolu-
19 tionary history and adaptations. Pochat-Cottilloux
20 (2024) presented a comprehensive review of diverse cro-
21 codylomorph groups. The paper emphasized how studies
22 associate variations in skull shapes, limb elements, and
23 dentition specializations with terrestrial adaptations. He
24 further comments on how the application of CT scan-
25 ning, bone histology, and geochemical analysis had been
26 widely utilized to advance our knowledge in the paleobi-
27 ology of extinct crocodylomorphs.

28 Continuing the efforts to establish the relationship
29 between morphological characteristics and lifestyle in
30 crocodylomorphs, this volume includes the work of Ruiz
31 et al. (2024), which described a new longirostrine Peiro-
32 sauridae, *Epoidesuchus tavaresae*, a crocodyliform from
33 the Late Cretaceous of Brazil. This contribution offers
34 phylogenetic and ecological perspectives on the group
35 and also discusses the possibility of two subgroups of
36 peirosaurids: the terrestrial and oreinirostrine Peirosauri-
37 nae and the longirostrine and semi-aquatic Pepesuchi-
38 nae. Moreover, it links longer snouts in Pepesuchinae to
39 evolutionary pressures to occupy aquatic habitats.

40 The contribution by Burke et al. (2024) investigates
41 the question of marine adaptations in gavialoids using
42 endocranial CT-scan data obtained for the European
43 Paleocene taxon *Eosuchus lerichei* for the first time.
44 Trans-oceanic separation from its sister taxon, found on
45 the coast of the United States, necessitated marine adap-
46 tations such as salt glands. However, physical evidence of
47 salt glands in extinct gavialoids is lacking, and extant
48 gavialoids do not possess them. CT data reveal concavities
49 on the deep surface of the prefrontal and lacrimal
50 bones, consistent with nasal salt glands. Thicker semi-
51 circular canals, when compared to the freshwater extant
52 *Gavialis*, further support a coastal ecology. Additionally,
53 by using new endocranial characters and reinterpreting

external anatomy, Burke et al. (2024) offer a revised phy- 54
55 logeny of Gavialoidea. They find it likely that marine
56 adaptations were plesiomorphic for Gavialoidea, but also
57 that there were numerous acquisitions or reductions in
58 these adaptations throughout the clade.

59 *Barreirosuchus franciscoi* is a peirosaurid that was
60 briefly described by Iori and Garcia (2012). Given that
61 the phylogeny of Notosuchia is still in the process of sta-
62 bilization, with several current competing hypotheses,
63 the discovery of new taxa and redescription of insuffi-
64 ciently described species are important. In this context,
65 Fachini et al. (2024) performed a detailed description of
66 the cranial elements, as well as phylogenetic and
67 morpho-functional analyses, of *B. franciscoi* from the
68 Late Cretaceous of the Bauru Group (southeast Brazil).
69 The phylogenetic reassessment shows that *Barreirosuchus*
70 belongs to the Itasuchidae clade (together with *Rukwasu-*
71 *chus yajabalajekundu*, *Pepesuchus deiseae*, and *Itasuchus*
72 *jesuinoi*) within Peirosauridae. Their morphological anal-
73 ysis suggests that *Barreirosuchus* was semiaquatic,
74 highlighting the diversity of lifestyles among Notosuchia.

75 While descriptions and phylogenetic studies of extinct
76 crocodylomorphs are characterized primarily by cranio-
77 dental features, Scavezoni et al. (2024) note that postcran-
78 ial anatomy remains understudied. In response, the
79 authors critically examine the thoracic girdle of aquatic
80 thalattosuchians and dyrosaurids to demonstrate the utili-
81 ty of postcranial characters for taxonomy, providing this
82 volume with detailed comparative descriptions in the
83 process. They find that many features of the scapula, cor-
84 acoid, and glenoid are dissimilar between the two groups,
85 vary intraspecifically, and supply information on taxon
86 ecology, development, and evolution. Scavezoni et al.
87 (2024) next use their girdle dataset of 191 characters to
88 build a postcrania-only phylogeny that includes Thalatto-
89 suchia, Dyrosauridae, and extant Crocodylia. The dataset
90 is able to recover clades and subclades, although often
91 with differing results from phylogenies that include cra-
92 nioidal characters. The authors emphasize that a signifi-
93 cant phylogenetic signal is present in pseudosuchian
94 postcrania and that postcranial characters should be
95 given more consideration.

96 Scheyer (2024) masterfully concludes our special vol-
97 ume with a survey of non-extant pseudosuchian paleobi-
98 ology studies and offers direction for further explorations.
99 He notes that scientific investigations of Pseudosuchia
100 are gaining momentum, citing the 2023 ICVM symposi-
101 um, "Paleohistological Inferences of Paleobiological
102 Traits in Pseudosuchia", as a recent product of this
103 increased interest. In his review, Scheyer (2024) empha-
104 sizes the importance of traditional as well as virtual
105 paleohistology techniques for studying pseudosuchians.
106 He observes that paleohistology is increasingly applied to

1 obtain empirical data rather than tissue descriptions
 2 alone, discussing recent applications to estimate genome
 3 size, life history, growth rates, and resting metabolic
 4 rates. However, Scheyer acknowledges that there are
 5 more discoveries to make. To illustrate this point, he
 6 notes that there are only around 80 paleohistology studies
 7 focused on pseudosuchians, compared with more than
 8 350 studies on Avemetatarsalia. Additionally, of the
 9 700 described species of pseudosuchians, only 126 have
 10 been sampled histologically thus far. In particular,
 11 Scheyer suggests that pseudosuchian paleohistology will
 12 benefit from increased exploration of intraskeletal varia-
 13 tion, further exploration of cranial and dental tissues,
 14 and additional discovery and collection of eggshell and
 15 otoliths for analyses. We are thus delighted for this
 16 opportunity to showcase new research on this fascinating
 17 group of archosaurs.


19 AUTHOR CONTRIBUTIONS

20 **Mariana Valeria de Araujo Sena:** Conceptualization;
 21 validation; visualization; writing – original draft;
 22 writing – review and editing. **Holly Noelle Woodward:**
 23 Conceptualization; validation; visualization; writing –
 24 original draft; writing – review and editing. **Jorge Cubo:**
 25 Conceptualization; validation; visualization; writing –
 26 original draft; writing – review and editing.

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