



HAL
open science

Pseudosuchia: Masters of survival and diversification

Mariana Valeria de Araujo Sena, Holly Noelle Woodward, Jorge Cubo

► **To cite this version:**

Mariana Valeria de Araujo Sena, Holly Noelle Woodward, Jorge Cubo. Pseudosuchia: Masters of survival and diversification. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, 2024, <10.1002/ar.25611>. <hal-04841427>

HAL Id: hal-04841427

<https://hal.sorbonne-universite.fr/hal-04841427v1>

Submitted on 17 Dec 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

Author Query Form

Journal: AR

Article: 25611

Dear Author,

During the copyediting of your manuscript the following queries arose.

Please refer to the query reference callout numbers in the page proofs and respond.

Please remember illegible or unclear comments and corrections may delay publication.

Many thanks for your assistance.

AUTHOR: Please note that missing content in references have been updated where we have been able to match the missing elements without ambiguity against a standard citation database, to meet the reference style requirements of the journal. It is your responsibility to check and ensure that all listed references are complete and accurate.

Query reference	Query	Remarks
Q1	AUTHOR: Kindly check and confirm if the correspondence details provided are appropriate.	
Q2	AUTHOR: Please verify that the linked ORCID identifiers are correct for each author. The ORCID IDs for 'Mariana Valeria de Araujo Sena' and 'Holly N Woodward' seem to be invalid. Please check and supply the correct ORCID IDs for these authors.	
Q3	AUTHOR: Please check and confirm if the inserted keywords are appropriate.	
Q4	AUTHOR: Please note that the Funding Name "European Commission" supplied has multiple matches in the funder Registry. Please indicate as to which one is the correct Funding Agency: "10.13039/100013268 – Directorate-General for Justice and Consumers"; "10.13039/100013271 – Consumer Programme"; "10.13039/100013273 – Directorate-General for Migration and Home Affairs"; "10.13039/100013284 – Executive Agency for Small and Medium-sized Enterprises"; "10.13039/100013971 – Directorate-General for International Partnerships"; "10.13039/100013972 – Directorate-General for Regional and Urban Policy".	
Q5	AUTHOR: Please provide the "volume number" for reference Burke et al., 2024.	
Q6	AUTHOR: Please provide the "volume number" for reference Cubo et al., 2024.	
Q7	AUTHOR: Please provide the "page range" for reference Fachini, Montefeltro, Godoy & Langer, 2024.	
Q8	AUTHOR: Please provide the "page range" for reference Farias et al., 2024.	
Q9	AUTHOR: Please provide the "page range" for reference Faure-Brac, 2024.	
Q10	AUTHOR: Please provide the "page range" for reference Heck & Woodward, 2024.	
Q11	AUTHOR: Please provide the "page range" for reference Johnson, Scheyer, Canoville & Maxwell, 2024.	
Q12	AUTHOR: Please provide the "page range" for reference Parker, Stocker, Reyes & Werning, 2024.	
Q13	AUTHOR: Please provide the "page range" for reference Pochat-Cottilloux, 2024.	

Q14	AUTHOR: Please provide the "volume number" for reference Ruiz et al., 2024.	
Q15	AUTHOR: Please provide the "page range" for reference Scavezzoni, Johnson, Jouve & Fischer, 2024.	
Q16	AUTHOR: Please provide the "volume number" for reference Scheyer, 2024.	
Q17	AUTHOR: Please provide the "volume number" for reference von Baczko, Zariwala, Ballentine, Desojo & Hutchinson, 2024.	
Q18	AUTHOR: Please provide the "volume number" for reference Woodward, Aubier, Sena & Cubo, 2024.	

INTRODUCTION

Pseudosuchia: Masters of survival and diversification

Mariana Valeria de Araujo Sena¹  | Holly Noelle Woodward²  | Jorge Cubo¹ 

¹Sorbonne Université, Muséum National d'Histoire Naturelle, CNRS, Centre de Recherche en Paléontologie – Paris (CR2P, UMR 7207), Paris, France

²Department of Anatomy and Cell Biology, Oklahoma State University – Center for Health Sciences, Tulsa, Oklahoma, USA

Correspondence

Mariana Valeria de Araujo Sena,
Sorbonne Université, Muséum National
d'Histoire Naturelle, CNRS, Centre de
Recherche en Paléontologie – Paris
(CR2P, UMR 7207), 4 Place Jussieu, Paris
75005, France.
Email: mari.araujo.sena@gmail.com

Funding information

European Commission, Grant/Award
Number: HORIZON-MSCA-2022-PF-
01-01 101107135

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 aetosaurs, 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 aetosaurs
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 aetosaurs, 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 ontog-
97 eny 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

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

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

62 Heck and Woodward (2024) tried to find proxies for 62
63 sex identification in extinct Pseudosuchia. As egg shell 63
64 formation requires a large amount of reserve calcium, 64
65 calcium metabolism may be a priori a powerful proxy for 65
66 this purpose. We know that birds utilize medullary bone 66
67 as a calcium reserve for egg-shelling. Heck and Wood- 67
68 ward (2024) hypothesized that crocodylians may mobilize 68
69 calcium ions from cortical bone and/or osteoderms, and 69
70 tried to use this process for sex identification purposes in 70
71 extinct Pseudosuchia. They analyzed undecalcified mid- 71
72 diaphyseal *Alligator mississippiensis* femoral bone cross- 72
73 sections and searched for cortical signals of reproduction 73
74 (i.e., evidence for resorptive processes linked to calcium 74
75 mobilization) but failed to find them. They concluded 75
76 that increasing the sample size and inclusion of speci- 76
77 mens with known reproductive histories may be neces- 77
78 sary for a more robust test of their hypothesis. 78

79 While many studies address the physiology of extinct 79
80 taxa by focusing on specific characteristics, Cubo et al. 80
81 (2024) emphasize an organismic approach to the ques- 81
82 tion. In this volume, the authors demonstrate their meth- 82
83 odology using femoral CT scans and thin-section 83
84 histology of the Early Jurassic metriorhynchoid *Pelago-* 84
85 *saurus typus*. The results were considered after applying 85
86 phylogenetic comparative methods. Bone compactness 86
87 values suggest an amphibious lifestyle, and the presence 87
88 of osteoderms with highly developed ornamentation indi- 88
89 cates periods of basking for thermoregulation. By esti- 89
90 mating the resting metabolic rate and red blood cell size, 90
91 they found *Pelagosaurus* to have an ectothermic thermo- 91
92 metabolism. Lastly, by exploring the maximum metabolic 92
93 rate and aerobic scope, Cubo et al. (2024) found that *Pela-* 93
94 *gosaurus* most likely employed sit-and-wait ambush tac- 94
95 tics or slow sustained subundulatory swimming, and 95
96 captured prey like the Gharial, using rapid lateral move- 96
97 ments of the head. 97

98 Woodward et al. (2024) propose a novel method to 98
99 retrodict the body mass of non-crocodylian pseudosu- 99
100 chians, based on a regression model using femur volume. 100
101 The authors suggest that this volumetric approach 101
102 reduces measurement errors and provides a more accu- 102
103 rate proxy for body mass estimation compared to tradi- 103
104 tional linear models. Their study, which is based on 104
105 *A. mississippiensis* body mass, was tested across individ- 105
106 uals from various crocodyliiform taxa. In large femora, 106

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.

28 ACKNOWLEDGMENTS

29 The Guest Editors express their gratitude to the Anatomical
 30 Record for the opportunity to contribute to this Special
 31 Issue. We extend our sincere thanks to all the
 32 authors who submitted their work, enriching the discus-
 33 sion within this publication. Special appreciation goes to
 34 the reviewers, whose professional insights and construc-
 35 tive feedback were invaluable. We are particularly grate-
 36 ful to The Anatomical Record Editorial Team, especially
 37 Heather F. Smith, Kim McKay, and Jeffrey Laitman, for
 38 their unwavering support and guidance throughout this
 39 project. Additionally, we acknowledge the contributions
 40 of the participants at ICVM 2023 in Cairns, Australia,
 41 whose discussions and insights have undoubtedly
 42 enriched this endeavor.

44 ORCID



45 **Mariana Valeria de Araujo Sena**  <https://orcid.org/0000-0003-4708-999X>

46 **Holly Noelle Woodward**  <https://orcid.org/0000-0003-0413-0681>

47 **Jorge Cubo**  <https://orcid.org/0000-0002-8160-779X>

51 REFERENCES

52 Benton, M. J., & Clark, J. M. (1988). Archosaur phylogeny and the
 53 relationships of the Crocodylia. In M. J. Benton (Ed.), *The*

- phylogeny and classification of Tetrapods Amphibians, reptiles, birds* (Vol. 1, pp. 295–338). Clarendon Press. 54
 55
 Benton, M. J., & Walker, A. D. (2002). *Erpetosuchus*, a crocodile-like 56
 basal archosaur from the Late Triassic of Elgin, Scotland. *Zoo-* 57
logical Journal of the Linnean Society, 136, 25–47.
 58
 Brusatte, S. L., Benton, M. J., Ruta, M., & Lloyd, G. T. (2008). Super- 59
 iority, competition, and opportunism in the evolutionary radi- 60
 ation of dinosaurs. *Science*, 321, 1485–1488.
 61
 Burke, P. M. J., Boerman, S. A., Perrichon, G., Martin, J. E., 62 
 Smith, T., Vellekoop, J., & Mannion, P. D. (2024). Endocranial 63
 anatomy and phylogenetic position of the crocodylian *Eosuchus* 64
lerichei from the late Paleocene of northwestern Europe and 65
 potential adaptations for transoceanic dispersal in gavialoids. 66
The Anatomical Record, 1–35.
 67
 Butler, R. J., Sullivan, C., Ezcurra, M. D., Liu, J., Lecuona, A., & 68
 Sookias, R. B. (2014). New clade of enigmatic early archosaurs 69
 yields insights into early pseudosuchian phylogeny and the bio- 70
 geography of the archosaur radiation. *BMC Evolutionary Biol-* 71
ogy, 14, 128.
 72
 Clark, J. M., Sues, H.-D., & Berman, D. S. (2001). A new specimen 73
 of *Hesperosuchus agilis* from the Upper Triassic of New Mexico 74
 and the interrelationships of basal crocodylomorph archosaurs. 75
Journal of Vertebrate Paleontology, 20, 683–704.
 76
 Crichton, M. (1991). *Jurassic park* (1st UK ed., p. 400). Century 77
 Publisher. 78
 79
 Cubo, J., Sena, M. V. A., Pellarin, R., Faure-Brac, M. G., Aubier, P., 80 
 Cheyron, C., Jouve, S., Allain, R., & Jalil, N.-E. (2024). Integra- 81
 tive paleophysiology of the metriorhynchoid *Pelagosaurus typus* 82
 (Pseudosuchia, Thalattosuchia). *The Anatomical Record*, 1–18. 83
 84
 Desojo, J. B., Heckert, A. B., Martz, J. W., Parker, W. G., 85
 Schoch, R. S., Small, B. J., & Sulej, T. (2013). Aetosauria: A 86
 clade of armoured pseudosuchians from the Upper Triassic 87
 continental beds. In S. J. Nesbitt, J. B. Desojo, & R. B. Irmis 88
 (Eds.), *Anatomy, phylogeny, and palaeobiology of early archo-* 89
sauurs and their kin (Vol. 379, pp. 203–239). Geological Society 90
 Special Publications. 91
 92
 Erickson, G. M., Gignac, P. M., Steppan, S. J., Lappin, A. K., 93
 Vliet, K. A., Brueggen, J. D., Inouye, B. D., Kledzik, D., & 94
 Webb, G. J. W. (2012). Insights into the ecology and evolution- 95
 ary success of crocodylians revealed through bite-force and 96
 tooth-pressure experimentation. *PLoS One*, 7, e31781. 97
 98
 Ezcurra, M. D. (2016). The phylogenetic relationships of basal arch- 99
 osauromorphs, with an emphasis on the systematics of protero- 100
 suchian archosauriforms. *PeerJ*, 4, e1778. 101
 102
 Fachini, T. S., Montefeltro, F., Godoy, P., & Langer, M. (2024). Cran- 103
 ial morphology and phylogenetic reassessment of *Barreirosu-* 104
chus franciscoi (Crocodylomorpha, Notosuchia), a Peirosauria 105
 from the Late Cretaceous of Brazil. *The Anatomical Record*, 1. 106
 107
 Farias, B., Carlisbino, T., Mastrantonio, B. M., Desojo, J. B. B., 108
 Schultz, C., & Soares, M. B. (2024). The first ontogenetic model 109
 for noncrocodylomorph loricatans, based on osteohistology of 110
 the ontogenetic series of *Prestosuchus chiniquensis* from the 111
 Middle Triassic of Brazil. *The Anatomical Record*, 1. 112
 113
 Faure-Brac, M. G. (2024). Pseudosuchian's thermophysiology: A 114
 review of the past two decades. *The Anatomical Record*, 1. 115
 116
 Foth, C., Ezcurra, M. D., Sookias, R. B., Brusatte, S. L., & Butler, R. 117
 (2016). Unappreciated diversification of stem archosaurs during 118
 the Middle Triassic predated the dominance of dinosaurs. *BMC* 119
Evolutionary Biology, 16, 188. 120

- Gauthier, J. A. (1986). Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, 8, 1–55.
- Gauthier, J. A., Nesbitt, S. J., Schachner, E. R., Bever, G. S., & Joyce, W. G. (2011). The bipedal stem crocodylian *Poposaurus gracilis*: Inferring function in fossils and innovation in archosaur locomotion. *Bulletin of the Peabody Museum of Natural History*, 52(1), 107–126.
- Gower, D. J. (2000). Rauisuchian archosaurs (Reptilia, Diapsida): An overview. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 218, 447–488.
- Heck, C. T., & Woodward, H. N. (2024). The consequences of calcium: Investigating intracortical reproductive signals in the American alligator for sex determination. *The Anatomical Record*, 1.
- Iori, F. V., & Garcia, K. L. (2012). *Barreirosuchus franciscoi*, um novo Crocodylomorpha Trematochampsidae da Bacia Bauru, Brasil. *Brazilian Journal of Geology*, 42(2), 397–410.
- Johnson, M., Scheyer, T., Canoville, A., & Maxwell, E. (2024). Palaeohistology of *Macrospondylus bollensis* (Crocodylomorpha: Thalattosuchia: Teleosauroidea) from the Posidonienschiefer Formation (Toarcian) of Germany, with insights into life history and ecology. *The Anatomical Record*, 1.
- Langston, W. J. (1973). The crocodylian skull in historical perspective. In C. Gans & T. S. Parsons (Eds.), *Biology of reptilia* (Vol. 4, pp. 263–289). Academic Press.
- Leardi, J. M., Pol, D., & Clark, J. M. (2020). Braincase anatomy of *Almadasuchus figarii* (Archosauria, Crocodylomorpha) and a review of the cranial pneumaticity in the origins of Crocodylomorpha. *Journal of Anatomy*, 237, 48–73.
- Lecuona, A., Desojo, J. B., & Cerda, I. A. (2020). New information on the anatomy and histology of *Gracilisuchus stipanicorum* (Archosauria: Pseudosuchia) from the Chañares Formation (early Carnian), Argentina. *Comptes Rendus Palevol*, 19, 40–62.
- Müller, R. T. (2024). A new small-sized predatory pseudosuchian archosaur from the Middle-Late Triassic of Southern Brazil. *Scientific Reports*, 14, 12706.
- Müller, R. T., von Baczko, M. B., Desojo, J. B., & Nesbitt, S. J. (2020). The first ornithosuchid from Brazil and its macroevolutionary and phylogenetic implications for Late Triassic faunas in Gondwana. *Acta Palaeontologica Polonica*, 65(1), 1–10.
- Nesbitt, S. J. (2011). The early evolution of archosaurs: Relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, 352, 1–292.
- Nesbitt, S. J., Brusatte, S. J., Desojo, J. B., Liparini, A., De Franca, M. A. G., Weinbaum, J. C., & Gower, D. J. (2013). Rauisuchia. In S. J. Nesbitt, J. B. Desojo, & R. B. Irmis (Eds.), *Anatomy, phylogeny and palaeobiology of early archosaurs and their kin* (Vol. 379, pp. 241–274). Geological Society, London, Special Publications.
- Nesbitt, S. J., Sidor, C., Irmis, R., Angielczyk, K. D., Smith, R. M. H., & Tsuji, L. A. (2010). Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature*, 464, 95–98.
- Parker, W. G., & Martz, J. W. (2011). The Late Triassic (Norian) Adamanian-Revueltian tetrapod transition in the Chinle Formation of Petrified Forest National Park, Arizona. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 101, 231–260.
- Parker, W. G., Nesbitt, S. J., Irmis, R. B., Martz, J. W., Marsh, A. D., Brown, M. A., Stocker, M. R., & Werning, S. (2021). Osteology and relationships of *Revueltosaurus callenderi* (Archosauria: Suchia) from the Upper Triassic (Norian) Chinle formation of Petrified Forest National Park, Arizona, United States. *The Anatomical Record*, 305, 2353–2414.
- Parker, W. G., Stocker, M., Reyes, W., & Werning, S. (2024). Anatomy and ontogeny of the “carnivorous aetosaur”: New information of *Coahomasuchus kahleorum* (Archosauria: Pseudosuchia) from the Upper Triassic Dockum Group of Texas. *The Anatomical Record*, 1.
- Pinheiro, F. L., Pretto, F. A., & Kerber, L. (2024). Special issue: The dawn of an era: Comparative and functional anatomy of triassic tetrapods. *The Anatomical Record*, 307, 4.
- Pochat-Cottilloux, Y. (2024). A review of the non semi-aquatic adaptations of extinct crocodylomorphs throughout their fossil record. *The Anatomical Record*, 1.
- Reyes, W. A., Martz, J. W., & Small, B. J. (2024). *Garzapelta muelleri* gen. et sp. nov., a new aetosaur (Archosauria: Pseudosuchia) from the late Triassic (middle Norian) middle Cooper Canyon Formation, Dockum Group, Texas, USA, and its implications on our understanding of the morphological disparity of the aetosaurian dorsal carapace. *The Anatomical Record*, 307(4), 1271–1299.
- Reyes, W. A., Parker, W. G., & Marsh, A. D. (2020). Cranial anatomy and dentition of the aetosaur *Typhothorax coccinarum* (Archosauria: Pseudosuchia) from the Upper Triassic (Revueltian–mid Norian) Chinle Formation of Arizona. *Journal of Vertebrate Paleontology*, 40(6), e1876080.
- Ruiz, J. V., Queiroz, M. V. L., Martins, K. C., Godoy, P. L., Iori, F. V., Langer, M. C., Montefeltro, F. C., & Bronzati, M. (2024). A new Peirosauridae (Crocodyliformes, Notosuchia) from the Adamantina Formation (Bauru Group, Late Cretaceous), with a revised phylogenetic analysis of Sebecia. *The Anatomical Record*, 1–24.
- Scavezzoni, I., Johnson, M., Jouve, S., & Fischer, V. (2024). Functional and phylogenetic signals in the pectoral girdle of Thalattosuchia and Dyrosauridae (Crocodylomorpha). *The Anatomical Record*, 1.
- Scheyer, T. M. (2024). The pseudosuchian record in paleohistology: A small review. *The Anatomical Record*, 1–12.
- Scheyer, T. M., Desojo, J. B., & Cerda, I. A. (2014). Bone histology of phytosaur, aetosaur, and other archosauriform osteoderms (Eureptilia, Archosauromorpha). *The Anatomical Record*, 297, 240–260.
- Sereno, P. C. (1991). Basal archosaurs: Phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology Memoir*, 2, 1–53.
- Spielberg, S. (Director). (1993). *Jurassic park*. [Film]. Universal Pictures.
- Taborda, J. R. A., Desojo, J. B., & Dvorkin, E. (2021). Biomechanical skull study of the aetosaur *Neoaeosauroides engaeus* using finite element analysis. *Ameghiniana*, 58, 401–415.
- Toljagic, O., & Butler, R. J. (2013). Triassic-Jurassic mass extinction as a trigger for the Mesozoic radiation of crocodylomorphs. *Biology Letters*, 9(3), 20130095.
- von Baczko, M. B., & Desojo, J. B. (2016). Cranial anatomy and palaeoneurology of the archosaur *Riojasuchus tenuisiceps* from the Los Colorados Formation, La Rioja, Argentina. *PLoS One*, 11(2), e0148575.
- von Baczko, M. B., Desojo, J. B., & Pol, D. (2018). Paleoneuroanatomy of the aetosaur *Neoaeosauroides engaeus* (Archosauria: 54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106

- 1 Pseudosuchia) and its paleobiological implications among arch- 54
 2 osauriforms. *PeerJ*, 6, e5456. 55
- 3 von Baczko, M. B., & Ezcurra, M. D. (2013). Ornithosuchidae: A 56
 4 group of Triassic archosaurs with a unique ankle joint. In S. J. 57
 5 Nesbitt, J. B. Desojo, & R. B. Irmis (Eds.), *Anatomy, phylogeny 58*
 6 *and palaeobiology of early archosaurs and their kin* (Vol. 379, 59
 7 pp. 187–202). Geological Society, London, Special Publications. 60
- Q17 7 von Baczko, M. B., Zariwala, J., Ballentine, S. E., Desojo, J. B., & 61
 8 Hutchinson, J. R. (2024). Biomechanical modeling of musculo- 62
 9 skeletal function related to the terrestrial locomotion of *Rioja-* 63
 10 *suchus tenuisiceps* (Archosauria: Ornithosuchidae). *The 64*
 11 *Anatomical Record*, 1–25. 65
- 12 Walker, E. P., Warnick, E., Lange, K. I., Uible, H. E., Hamlet, S. E., 66
 13 Davis, M. A., & Wright, P. E. (1964). *Mammals of the world 67*
 14 (Vol. II, pp. 1321–1408). Johns Hopkins Press. 68
- 15 Watson, D. M. S. (1917). A sketch-classification of the pre-Jurassic 69
 16 tetrapod vertebrates. *Proceedings of the Zoological Society of 70*
 17 *London, 1917*, 167–186. 71
- Q18 17 Woodward, H. N., Aubier, P., Sena, M. V. A., & Cubo, J. (2024). 72
 18 Evaluating extinct pseudosuchian body mass estimates 73
 19 using a femur volume-based model. *The Anatomical Record*, 74
 20 1–9. 75
 21 Wu, X. C., & Russell, A. P. (2001). Redescription of *Turfanosuchus 76*
 22 *dabanensis* (Archosauriformes) and new information on its 77
 23 phylogenetic relationships. *Journal of Vertebrate Paleontology*, 78
 24 21, 40–50. 79
 25 Young, C. C. (1973). On a new pseudosuchian from Turfan, Sinkiang 80
 26 (Xinjiang). *Memoirs of the Institute of Vertebrate Paleontology 81*
 27 *and Paleoanthropology of the Academia Sinica, Series B*, 10, 82
 28 15–37. 83
 29 84
 30 85
 31 86
 32 87
 33 88
 34 89
 35 90
 36 91
 37 92
 38 93
 39 94
 40 95
 41 96
 42 97
 43 98
 44 99
 45 100
 46 101
 47 102
 48 103
 49 104
 50 105
 51 106
 52
 53

How to cite this article: Sena, M. V. A., Woodward, H. N., & Cubo, J. (2024). Pseudosuchia: Masters of survival and diversification. *The Anatomical Record*, 1–7. <https://doi.org/10.1002/ar.25611>

Uncorrected Proof