

Migrations, diversifications and extinctions: the evolutionary history of crocodyliforms in Australasia

Jorgo Ristevski , Paul M. A. Willis, Adam M. Yates , Matt A. White , Lachlan J. Hart , Michael D. Stein , Gilbert J. Price , and Steven W. Salisbury 

ABSTRACT

Crocodyliform palaeontology in Australasia has a productive research record that began in the late nineteenth century and continues today. In this study, we summarize the current understanding on the taxonomic diversity and phylogenetic relationships of Australasian crocodyliforms based on first-hand knowledge of relevant fossil material and a review of the published literature. The currently known fossil record of Crocodyliformes in Australasia spans more than 113 million years, from the Early Cretaceous to the Holocene, and largely consists of body fossils discovered on continental Australia. Whilst only two crocodyliform genera are recognized from Australasia's Mesozoic, the Cenozoic is distinguished by a remarkable taxonomic diversity of crocodylian crocodyliforms. By far the most common crocodylians from Australasia are members of Mekosuchinae, whose fossils are unambiguously known from the early Eocene until the Holocene. In addition to mekosuchines, during the Cenozoic Australasia was also inhabited by gavialoids and species of *Crocodylus*, with four extant species of the latter being the only surviving crocodylians in Australia and New Guinea. The phylogenetic relationships of Australasia's crocodylians, particularly mekosuchines, have been a topic of interest to palaeontologists for over two decades. We performed several phylogenetic analyses to test the relationships of Mekosuchinae and other extinct crocodylians. Most results from our analyses found Mekosuchinae as a basal crocodyloid clade within Longirostres. However, some of the results recovered an alternative position for the majority of mekosuchines outside of Longirostres and the Late Cretaceous–early Paleogene Orientalosuchina as its deeply nested subclade. These results suggest that Mekosuchinae had its origins in Asia during the Cretaceous, and that mekosuchines arrived from southeast Asia into Australia no later than the late Paleocene. If this hypothesis is correct, then Mekosuchinae would no longer be an Australasian endemic clade since mekosuchines also seem to have persisted on continental Asia until the late Eocene.

ARTICLE HISTORY

Received 28 August 2022
Revised 14 February 2023
Accepted 6 April 2023

KEYWORDS

Crocodylia; *Crocodylus*;
Crocodyliformes;
Gavialoidea; Longirostres;
Mekosuchinae;
Orientalosuchina

Jorgo Ristevski [jorgo.ristevski@gmail.com], School of Biological Sciences, The University of Queensland, Brisbane, 4072, Queensland, Australia; Paul M. A. Willis [paul@palaeopictures.com], School of Biological Sciences, Flinders University, Adelaide, 2100, South Australia, Australia; Adam M. Yates [Adamm.Yates@magnt.net.au], Museum of Central Australia, Museum and Art Gallery of the Northern Territory, Alice Springs, 0870, Northern Territory, Australia; Matt A. White [fossilised@hotmail.com], Palaeoscience Research Centre, University of New England, Armidale, 2351, New South Wales, Australia, Australian Age of Dinosaurs Museum of Natural History, The Jump-Up, Winton, 4735, Queensland, Australia; Lachlan J. Hart [l.hart@unsw.edu.au], Earth and Sustainability Science Research Centre, School of Biological, Earth and Environmental Sciences (BEES), University of New South Wales, Kensington, 2052, New South Wales, Australia, Australian Museum Research Institute, 1 William Street, Sydney, 2010, New South Wales, Australia; Michael D. Stein [michael.stein@unswalumni.com], Earth and Sustainability Science Research Center, School of Biological, Earth and Environmental Sciences (BEES), University of New South Wales, Kensington, 2052, New South Wales, Australia; Gilbert J. Price [g.price1@uq.edu.au], School of Earth and Environmental Sciences, The University of Queensland, Brisbane, 4072, Queensland, Australia; Steven W. Salisbury [s.salisbury@uq.edu.au], School of Biological Sciences, The University of Queensland, Brisbane, 4072, Queensland, Australia.

CROCODYLOMORPHA is a hugely successful pseudosuchian archosaur clade with a long fossil record spanning more than 200 million years (Ma) from the Late Triassic (~235 Ma, Carnian) to present day (Irmis *et al.* 2013, Zanno *et al.* 2015). Throughout their evolutionary history, crocodylomorphs evolved into a variety of morphotypes that allowed

them to exploit different habitats and ecological niches, some of which are unparalleled by extant taxa (e.g., Sereno *et al.* 2001, Salisbury *et al.* 2006, Paolillo & Linares 2007, Kley *et al.* 2010, Pol & Leardi 2015, Dal Sasso *et al.* 2017, Godoy *et al.* 2019, Melstrom & Irmis 2019, Wilberg *et al.* 2019). The remarkable taxonomic and morphological diversity of Crocodylomorpha and its subset Crocodyliformes reached its zenith during the Mesozoic (Godoy *et al.* 2019, Wilberg *et al.* 2019). Today, there are fewer than 30 recognized species of extant crocodyliforms – all belonging to the eusuchian subclade Crocodylia – that inhabit the tropical and/or sub-tropical regions of Africa, the Americas, Asia and Australia (Grigg & Kirshner 2015). In contrast to past diversity during the Cenozoic and especially the Mesozoic,

This article has been corrected with minor changes. These changes do not impact the academic content of the article.

© 2023 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

all extant crocodylians are semi-aquatic ambush predators that range from ≤ 2 m to over 6 m in total length (TL).

Present-day Australasia is inhabited by four crocodylian species that belong to the genus *Crocodylus* Laurenti 1768. In Australia these are *Crocodylus johnstoni* (Kreff 1873) and *Crocodylus porosus* Schneider 1801 (Fig. 1). *Crocodylus johnstoni* (Fig. 1A) is the only extant crocodylian that is endemic to Australia, inhabiting the northern mainland of the continent (Isberg *et al.* 2017). *Crocodylus porosus* (Fig. 1B) inhabits a vast range in the Indo-Pacific region, including northern Australia, India, parts of southeast Asia, New Guinea, and Vanuatu (Webb *et al.* 2021). *Crocodylus porosus*

is also the largest living reptile and is capable of attaining a TL of more than 6 m and can weigh over a metric ton (Grigg & Kirshner 2015). Besides *C. porosus*, the island of New Guinea is also home to two endemic species of *Crocodylus*, *Crocodylus novaeguineae* (Schmidt, 1928) and the recently named *Crocodylus halli* Murray, Russo, Zorilla & McMahan, 2019. Unlike the current diversity, Australasia's fossil record attests to a significantly richer taxonomic composition of crocodyliforms from the Mesozoic and more so from the Cenozoic (Willis 2006). Crocodyliform fossils (predominantly body fossils, with few ichnofossils: e.g., Willis 2006, Poropat *et al.* 2021) are known

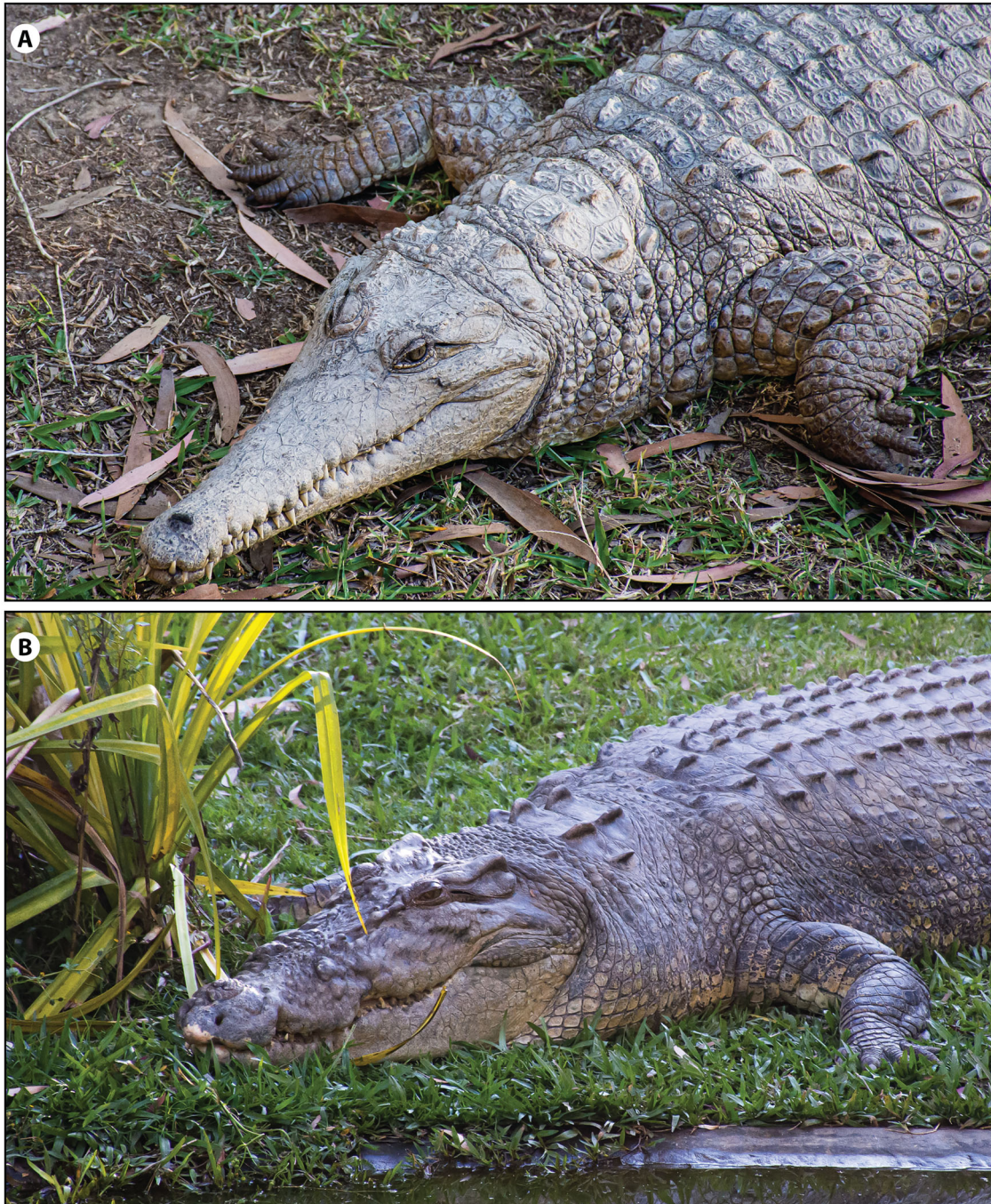


Figure 1. Extant *Crocodylus* from Australasia. A, *Crocodylus johnstoni*. B, *Crocodylus porosus*.

from numerous localities across Australasia, and most come from continental Australia (Fig. 2). Thus far, there are only two named crocodyliform genera from the Mesozoic of Australasia, and both are from the Cretaceous of continental Australia (Salisbury *et al.* 2006, Hart *et al.* 2019, Hart 2020, White *et al.* 2022). On the other hand, the known taxonomic diversity from Australasia's Cenozoic is much greater, with 12 formally named crocodylian genera (excluding

Crocodylus: Fig. 3). The vast majority of Australasia's Cenozoic crocodylians belong to the now extinct clade Mekosuchinae, which are known from the early Eocene (Willis *et al.* 1993, Salisbury & Willis 1996, Holt *et al.* 2005, Buchanan 2009) to the Holocene (Balouet 1991, Mead *et al.* 2002). No mekosuchine crocodylians are known from continental Australia after the Late Pleistocene (Molnar 1982c, Willis & Molnar 1997a, 1997b, Ristevski *et al.* 2020a),

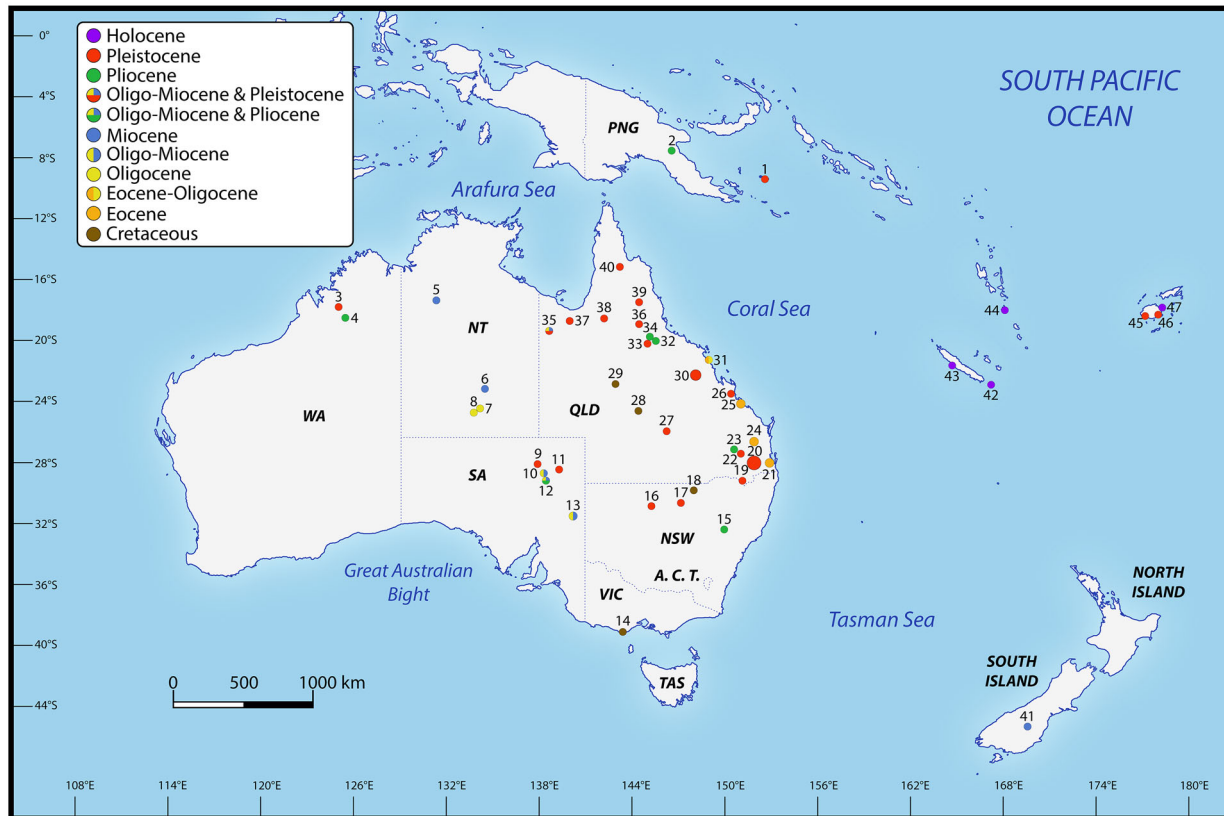


Figure 2. Australasian fossil crocodyliform localities. (1) Busai, Muyua, Papua New Guinea (de Vis 1905, Molnar 1982a); (2) Awe Fauna, Otibanda Formation, Papua New Guinea (Plane 1967); (3) Windjana Gorge, Western Australia (Gorter & Nicoll 1978); (4) Qunbun Local Fauna, Western Australia (Flannery 1984); (5) Bullock Creek, Northern Territory (Willis *et al.* 1990, Megirian *et al.* 1991, Murray & Megirian 1992, Megirian 1994, Stein *et al.* 2017, 2020, Yates 2017); (6) Alcoota Station, Northern Territory (Stirton 1967, Woodburne 1967, Murray & Megirian 1992, Murray *et al.* 1993, Megirian *et al.* 1996, Stein *et al.* 2017, Yates 2017); (7) Kangaroo Well Local Fauna, Ulta Limestone, Northern Territory (Megirian *et al.* 2004); (8) Pwerte Marnte Marnte Local Fauna, Northern Territory (Murray & Megirian 2006, Yates 2017); (9) Warburton River, South Australia (Willis & Molnar 1997a); (10) Wipajiri Formation, Lake Ngapakaldi, South Australia (Stirton *et al.* 1961, 1967, Willis & Molnar 1991b); (11) Cooper's Creek, South Australia (Willis & Molnar 1997a, Vickers-Rich & Rich 1999); (12) Lake Palankarinna, Etadunna Formation (Stirton *et al.* 1961, Willis & Molnar 1991b), Tirari Formation, and Mampuwordu Sands, South Australia (Hecht & Archer 1977, Yates & Pledge 2017); (13) Lakes Pinpa and Tarkarooloo, Namba Formation, South Australia (Willis & Molnar 1991b). (14) Dinosaur Cove, Otway Ranges, Eumeralla Formation, Victoria (Willis 1997b, Salisbury *et al.* 2003, Poropat *et al.* 2018, Paragnani *et al.* 2019); (15) Krui River Local Fauna, New South Wales (Molnar 1991); (16) Myrtle Vale, New South Wales (Thompson 1980, Willis & Molnar 1997a); (17) Cuddie Springs, New South Wales (Dodson *et al.* 1993); (18) Griman Creek Formation, Lightning Ridge, New South Wales (Etheridge 1917, Molnar 1980, Molnar & Willis 2001, Hart 2020, Hart *et al.* 2019, 2021); (19) Texas Caves, Queensland (Hecht & Archer 1977, Archer 1978, Molnar 1982c); (20) Multiple localities on the Darling Downs (King Creek, west of Pilton, Westbrook or Gowrie Creek, Toowoomba Region), Queensland (Lydekker 1888, Molnar 1982c, Sobbe *et al.* 2013, Ristevski *et al.* 2020a, 2021); (21) Geebung, Runcorn, Eight Mile Plains and Redbank Plains, Brisbane area, Queensland (Jones 1927, Riek 1952, Willis & Molnar 1991a); (22) Macalister, Queensland (Longman 1928, Molnar 1982b, Willis & Molnar 1997a); (23) Chinchilla, Queensland (de Vis 1886, Hill *et al.* 1970, Gorter & Nicoll 1978, Molnar 1982b, 1982c, Willis & Molnar 1997a, Mackness *et al.* 2010, Louys & Price 2015, Chiotakis 2018, Ristevski *et al.* 2020a, Campbell *et al.* 2021) and Brigalow, Queensland (Longman 1929); (24) Tingamarra Local Fauna, Murgon, Queensland (Molnar 1982b, Willis *et al.* 1993, Salisbury & Willis 1996, Stein *et al.* 2012, 2020); (25) The Narrows Graben, near Gladstone, Queensland (Hills 1943, Coshell 1986, Holt *et al.* 2005, Buchanan 2008, 2009, Stein *et al.* 2017); (26) Mt. Etna region, Queensland (Hocknull 2009); (27) Lansdowne Station, near Tambo, Queensland (Longman 1925); (28) Winton Formation, near Isisford, Queensland (Salisbury *et al.* 2006, Syme & Salisbury 2018); (29) Winton Formation at Elderslie Station (White *et al.* 2022) and Karoola Station (Poropat *et al.* 2021); (30) South Walker Creek (Hocknull *et al.* 2020) and near the Nebo district (Willis & Molnar 1997a), Queensland; (31) Cape Hillsborough, Queensland (McNamara 1993); (32) Bluff Downs Local Fauna, Allingham Formation, Queensland (Archer in Archer & Wade 1976, Molnar 1979, Willis & Mackness 1996, Mackness & Sutton 2000); (33) Wyandotte Local Fauna, Wyandotte Formation, Queensland (McNamara 1990); (34) Tara Creek, near Maryvale, Queensland (Longman 1924, Willis & Molnar 1997a, Molnar 1982c); (35) Riversleigh World Heritage Area, Queensland (Willis & Archer 1990, Willis *et al.* 1990, Willis 1993b, 1995, 1997a, 2001, Willis & Molnar 1997a, Scanlon 2006a, 2014, Yates 2017, Stein *et al.* 2015, 2016, 2017, 2020, Ristevski *et al.* 2023); (36) "Rosella Plains" Station, Queensland (Molnar 1982c); (37) Floraville Downs Station, Queensland (Willis & Archer 1990, Willis & Molnar 1997a, Molnar *et al.* 2017, Ristevski *et al.* 2019, Stein *et al.* 2020); (38) "Alehvale" Station, Croydon area (Molnar 1982c); (39) Tea Tree Cave, Chillagoe area, Queensland (Molnar 1982c); (40) "Glen Garland" Station, Queensland (Molnar 1982c); (41) Bannockburn Formation, South Island, New Zealand (Molnar & Pole 1997, Salisbury *et al.* 2017); (42) Kanumera, Isle of Pines, New Caledonia (Buffetaut 1983, Balouet & Buffetaut 1987); (43) Pindai Caves, Grande Terre, New Caledonia (Balouet & Buffetaut 1987, Anderson *et al.* 2010, Salisbury *et al.* 2010); (44) Arapus and Teouma archaeological sites, Efate, Vanuatu (Mead *et al.* 2002, Hawkins 2015); (45) Voli Voli Cave, Viti Levu, Fiji (Molnar *et al.* 2002); (46) Wainibuku Cave, Viti Levu, Fiji (Molnar *et al.* 2002); (47) Naigani, Fiji (Irwin *et al.* 2011).

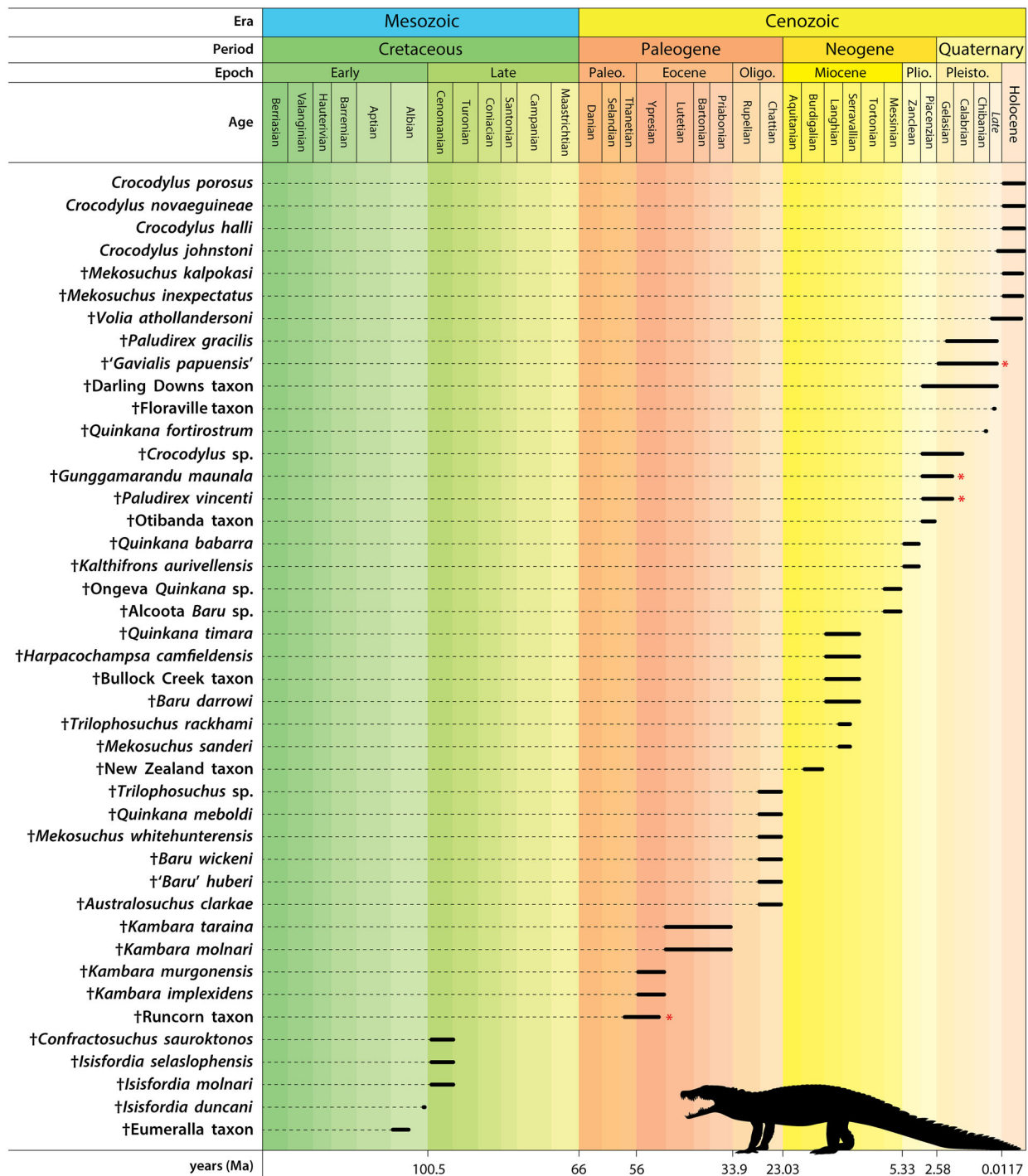


Figure 3. Stratigraphical age ranges of documented Australasian crocodyliform taxa. Red asterisk * denotes the uncertain late Paleocene to early Eocene age of the 'Runcorn taxon'; Pliocene–Pleistocene *Gunggamarandu maunala*; mid-Pliocene to ?Late Pleistocene *Paludirex vincenti*; ?Pleistocene *Gavialis papuensis*. Information from the Paleobiology Database (<https://paleobiodb.org>) accessed on 11 July 2022. Numerical ages from version 2021/10 of the International Chronostratigraphic Chart (<https://stratigraphy.org/chart>). Abbreviations: Oligo., Oligocene; Paleo., Paleocene; Pleisto., Pleistocene; Plio., Pliocene.

although few insular mekosuchines from the South Pacific managed to survive into the Holocene until their extinction not long after human colonization (Balouet & Buffetaut 1987, Balouet 1989, 1991, Mead *et al.* 2002, Molnar *et al.* 2002). Multiple studies published in the past three decades have demonstrated the importance of Mekosuchinae in a global context of crocodylian evolution, systematics, palaeobiogeography, and even implications for reptile extinctions due to anthropogenic factors (e.g., Mead *et al.* 2002, Willis 2006, Lee & Yates 2018, Rio & Mannion 2021).

Historical overview

Beginnings: nineteenth century to 1977

Crocodyliform palaeontology in Australasia has its origins in the nineteenth century. The publication by Clarke (1869) contains the earliest report of crocodylian fossils from continental Australia, with a brief mention of crocodylian remains found at Crinum Creek near Peak Downs in Queensland. According to Clarke (1869), this material was sent to Thomas Huxley in England; however, there is no

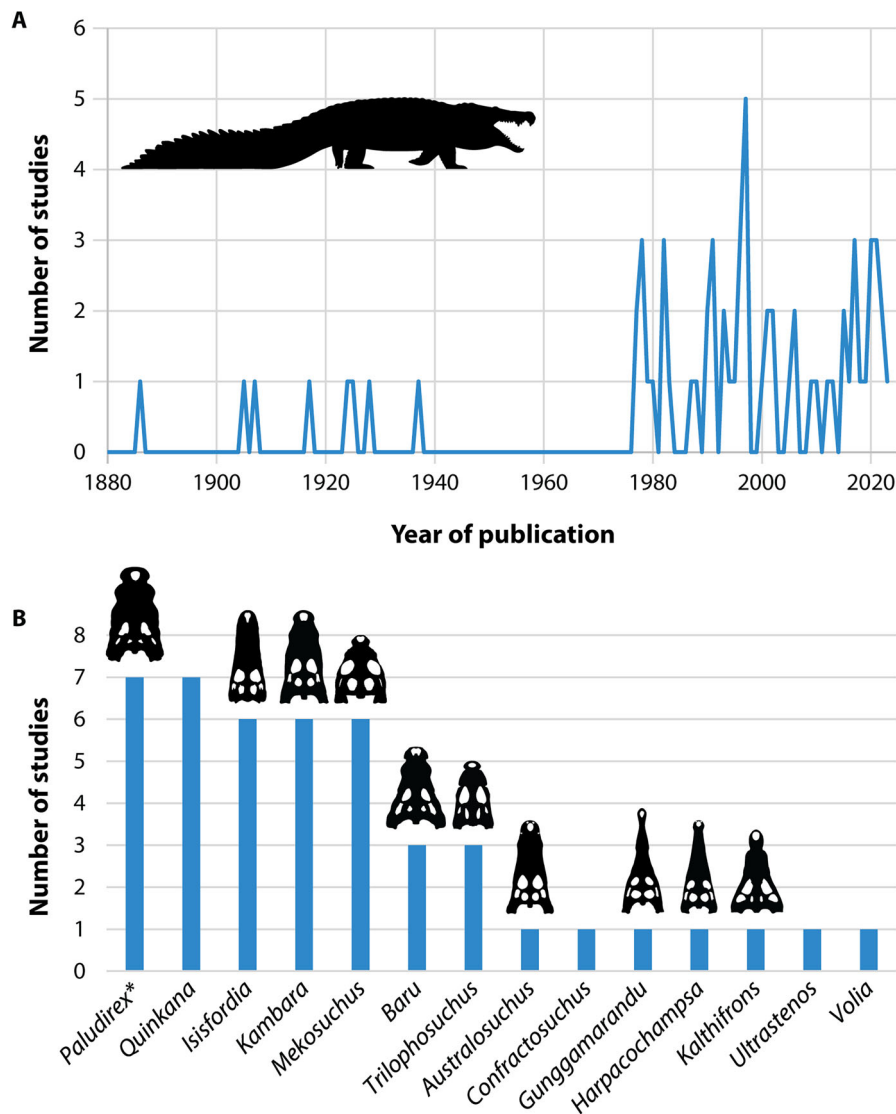


Figure 4. Published studies on Australasian crocodyliforms. **A**, Peer-reviewed articles exclusively documenting or containing substantial information about Australasian crocodyliforms. Conference abstracts, unpublished theses, and non-peer reviewed articles are excluded. **B**, Number of formally published peer-reviewed articles dedicated to a single extinct crocodyliform genus from Australasia. *Combined articles dedicated to *Paludirex* and '*Pallimnarchus*'. Silhouette of *Paludirex vincenti* in A from PhyloPic by Armin Reindl. For more information see Supplemental Data S1.

mention of these fossils in the works by Huxley. The second report is by Daintree (1872), who mentioned isolated crocodylian teeth that he referred to as '*Crocodylus australis*' (note the archaic spelling of *Crocodylus*). Later, Jack & Etheridge (1892) would reassign the material mentioned by Daintree (1872) to *Crocodylus porosus*. Lydekker (1888) would also provide brief mentions of crocodylian material from Australia that was shipped to the British Museum of Natural History in London. Lydekker (1888) assigned this material to *C. porosus*, although more recent examinations of the same indicate that such referral is erroneous (Willis 1997b, 2006). The most significant study from the nineteenth century was published by de Vis (1886), where he provided the first detailed description of an extinct crocodylian from Australia. Therein, he described several craniomandibular and postcranial fragments that were discovered on the Darling Downs in southeastern Queensland, and informally proposed the

binomen *Pallimnarchus pollens* de Vis, 1886. Despite its informal establishment, usage of the generic name *Pallimnarchus* de Vis, 1886 would become relatively common throughout the twentieth century and several authors would proceed to refer additional specimens to this genus (see Ristevski *et al.* 2020a for detailed review). Work on Australasian crocodyliforms was somewhat sporadic during the first half of the twentieth century (Fig. 4A; see also Willis 1993a). Significant works from the early twentieth century include the description of gavialoid remains from Muya (de Vis 1905), the first report of a Cretaceous crocodyliform from Australia (Etheridge 1917), and several publications by Longman (1924, 1925, 1928, 1929) on Cenozoic crocodylians. Studies devoted exclusively, or at least in large part, to extinct Australasian crocodylians ceased publication between 1937 and 1977, even though there were occasional studies that mentioned crocodylian fossils (e.g., Riek 1952, Plane 1967, Woodburne 1967, Hill *et al.* 1970; see Fig. 4A).

Renaissance: 1977–1990

Crocodyliform palaeontology in Australasia would experience a renaissance in 1977. The papers published that year by Hecht & Archer (1977) and Molnar (1977) ended the 40-year hiatus on crocodyliform-focused studies from Australasia. Furthermore, ever since 1977, studies on crocodyliforms from this part of the planet would become more frequent and conducted on a fairly regular basis (Fig. 4A; Supplemental Data S1). Some of the most significant studies from this period were published by Ralph E. Molnar (Molnar 1979, 1980, 1982a, 1982b, 1982c). The most important study from this time is the description and naming of a second extinct crocodylian genus from Australia, *Quinkana* Molnar, 1982c. Although described from an incomplete but well-preserved snout, the discovery of *Quinkana fortirostrum* Molnar, 1982c identified the presence of altirostral (i.e., tall-snouted = oreinirostral *sensu* Busbey, 1995) crocodylians from Australia. Furthermore, Molnar (1982c) described isolated ziphodont (i.e., labiolingually compressed and serrated) teeth from crocodylians dating to the Pleistocene. Thus, the Pleistocene age of its type material currently makes *Q. fortirostrum* the youngest formally named and described ziphodont crocodyliform in the world. Also during this period, Molnar (1982b) would provide a revision of '*Pallimnarchus pollens*' and designate a lectotype specimen for this taxon, thus commencing the disentanglement of the Pliocene–Pleistocene crocodylian complex from Australia. Outside of Australia, Buffetaut (1983) reported of crocodylian fossils from New Caledonia that would later lead to the naming of the eminent taxon *Mekosuchus inexpectatus* Balouet & Buffetaut, 1987. The combination of unique morphological features in *M. inexpectatus* (read below) was used as a basis for the proposal of Mekosuchidae by Balouet & Buffetaut (1987). At first, *M. inexpectatus* was the only taxon referred to Mekosuchidae, and its exact placement within Crocodylia was unclear (Balouet & Buffetaut 1987). It is important to note that at the time, crocodylian phylogenetic systematics were still in their infancy with studies dedicated to crocodylian systematics (e.g., Clark in Benton & Clark 1988, Norell & Clark 1990, Clark & Norell 1992) published subsequent to the paper by Balouet & Buffetaut (1987). Nevertheless, the discovery of this unique insular species from the Quaternary of the South Pacific would cement Australasia as a region of great importance to the understanding of crocodylian evolution.

Modern crocodyliform palaeontology in Australasia: 1990–present

The early 1990s may be regarded as the advent of modern crocodyliform palaeontology in Australasia in general and Australia in particular, as this period witnessed a surge of studies that laid the foundation for much of today's understanding on the evolution of Crocodylia in the region (Fig. 4A; Supplemental Data S1). It was during this time that PMAW and SWS both began publishing material derived from their theses. Other notable work from this period was authored by Megirian (1994) and Megirian *et al.* (1991).

Five new Cenozoic crocodylian genera were named and described between 1990 and 1993: *Baru* Willis, Murray & Megirian, 1990, *Australosuchus* Willis & Molnar, 1991b, *Harpacochampsia* Megirian, Murray & Willis, 1991, *Kambara* Willis, Molnar & Scanlon, 1993, and *Trilophosuchus* Willis, 1993b. The presence of several morphological features shared between some Australian fossil taxa led Willis *et al.* (1990) to propose the concept of the so-called Australian Tertiary crocodylian radiation. Originally, the Australian Tertiary crocodylian radiation included '*Pallimnarchus pollens*', *Quinkana fortirostrum* and *Baru darrowi* Willis, Murray & Megirian, 1990. Later, the Australian radiation was revised and expanded with the inclusion of *Australosuchus* by Willis & Molnar (1991b), before the concept was replaced with the defining of Mekosuchinae as a subfamily of Crocodylidae by Willis *et al.* (1993). The establishment of Mekosuchinae was a revision to the previously proposed Mekosuchidae by Balouet & Buffetaut (1987), which was regarded as a sister taxon to modern Crocodylia by the latter. Mekosuchinae was proposed for several taxa endemic to Australasia (*Mekosuchus inexpectatus*, *Quinkana fortirostrum*, '*Pallimnarchus pollens*', *Baru darrowi*, *Australosuchus clarkae* Willis & Molnar 1991b, and *Kambara murgonensis* Willis, Molnar & Scanlon, 1993). Since then, the taxonomic composition of Mekosuchinae would expand significantly with the addition of more genera and species (*Kalthifrons aurivellensis* Yates & Pledge, 2017, *Trilophosuchus rackhami* Willis, 1993b, *Ultrastenos willisi* Stein, Hand & Archer, 2016, *Volia athollandersoni* Molnar, Worthy & Willis, 2002, and 12 new species within previously established genera). Salisbury & Willis (1996) were the first to publish a comprehensive phylogenetic assessment of Mekosuchinae, and they also erected the mekosuchine sub-clade Mekosuchini.

With five publications on Australasian crocodylians, the year 1997 has been the most productive to date (Molnar & Pole 1997, Willis 1997a, 1997b, Willis & Molnar 1997a, 1997b; see Fig. 4A). Outside of Australia, Molnar & Pole (1997) described a crocodylian angular from New Zealand/Aotearoa, thus definitively proving the presence of Crocodylia in New Zealand. Some insular mekosuchines were named in the early 2000s, one from Vanuatu (*Mekosuchus kalpokasi* Mead, Steadman, Bedford, Bell & Spriggs, 2002) and another from Fiji (*V. athollandersoni*). The year 2006 saw the naming and description of *Isisfordia duncani* Salisbury, Molnar, Frey & Willis, 2006, which is the most complete known crocodyliform from Australasia. Recently, two additional species were referred to this genus (Hart *et al.* 2019, Hart 2020) and a second crocodyliform genus from the Mesozoic of Australia, *Confractosuchus* White, Bell, Campione, Sansalone, Brougham, Bevitt, Molnar, Cook, Wroe & Elliott, 2022, was named and offered further insights into the taxonomic composition of crocodyliforms from Australia's Mesozoic. The early–mid 2010s saw the publication of several studies published by MDS as derived from the work in his PhD thesis, and several studies authored by AMY. In the early 2020s, JR authored several publications derived from the work in his PhD thesis. The

taxonomic status of ‘*Pallimnarchus*’ was recently re-evaluated, and this genus is considered a *nomen dubium*. Some specimens formerly assigned to ‘*Pallimnarchus*’ were assigned to a new genus named *Paludirex* Ristevski, Yates, Price, Molnar, Weisbecker & Salisbury, 2020a. In addition to mekosuchines and species of *Crocodylus*, Australia was also inhabited by gavialoids, *Harpacochamps* and *Gunggamarandu* Ristevski, Price, Weisbecker & Salisbury, 2021 (Megirian *et al.* 1991, Lee & Yates 2018, Ristevski *et al.* 2023). Although several authors of this paper have multiple publications on Australasian crocodyliforms, the most prolific has been Ralph E. Molnar, with 11 studies as the sole or lead author, and who has contributed as a co-author on numerous studies from 1977 to 2022 (see lists of all formally

named crocodyliforms from Australasia in Tables 1, 2). Out of the 14 currently recognized extinct crocodyliform genera from Australasia, ‘*Pallimnarchus*’ (including publications on *Paludirex*) and *Quinkana* have had the greatest number of studies dedicated exclusively to their species (Fig. 4B; Supplemental Data S1).

Materials and methods

Phylogenetic analyses

The phylogenetic assessments undertaken in this study are based on the character matrix by Ristevski *et al.* (2023), which is an updated and expanded version of the matrices

Table 1. List of crocodyliform taxa from Australasia (classification based on the results from Fig. 24).

CROCODYLIFORMES Hay, 1930 (<i>sensu</i> Sereno <i>et al.</i> , 2001)
CROCODYLIFORMES Hay, 1930 (<i>sensu</i> Sereno <i>et al.</i> , 2001)
MESOECROCODYLIA Whetstone & Whybrow, 1983 (<i>sensu</i> Sereno <i>et al.</i> , 2001)
NEOSUCHIA Benton & Clark, 1988 (<i>sensu</i> Sereno <i>et al.</i> , 2001)
† <i>Confractusuchus sauroktonos</i> White <i>et al.</i> , 2022
† SUSISUCHIDAE Salisbury <i>et al.</i> , 2003
† <i>Isisfordia duncani</i> Salisbury <i>et al.</i> , 2006
† <i>Isisfordia molnari</i> Hart <i>et al.</i> , 2019
† <i>Isisfordia selaslophensis</i> (Etheridge, 1917) Hart, 2020
=† <i>Crocodylus</i> (? <i>Botosaurus</i>) <i>selaslophensis</i> Etheridge, 1917
=† <i>Crocodylus</i> (<i>Bottosaurus</i>) <i>selaslophensis</i> (Etheridge, 1917) Molnar, 1980
EUSUCHIA Huxley, 1875
CROCODYLIA Gmelin, 1789 (<i>sensu</i> Clark in Benton & Clark, 1988)
LONGIROSTRES Harshman <i>et al.</i> , 2003
GAVIALOIDEA Hay, 1930
† <i>Gavialis papuensis</i> de Vis, 1905
† <i>Gunggamarandu maunala</i> Ristevski <i>et al.</i> , 2021
† <i>Harpacochamps camfieldensis</i> Megirian <i>et al.</i> , 1991
CROCODYLOIDEA Fitzinger, 1826 (<i>sensu</i> Brochu, 2003)
† MEKOSUCHINAE Willis <i>et al.</i> , 1993
† <i>Australosuchus clarkae</i> Willis & Molnar, 1991b
† <i>Kalthifrons aurivellensis</i> Yates & Pledge, 2017
† <i>Kambara implexidens</i> Salisbury & Willis, 1996
† <i>Kambara molnari</i> Holt <i>et al.</i> , 2005
† <i>Kambara murgonensis</i> Willis <i>et al.</i> , 1993
† <i>Kambara taraina</i> Buchanan, 2009
† MEKOSUCHINI Salisbury & Willis, 1996
† <i>Baru</i> <i>huberi</i> Willis, 1997a
† <i>Baru darrowi</i> Willis <i>et al.</i> , 1990
† <i>Baru wickeni</i> Willis, 1997a
† <i>Mekosuchus inexpectatus</i> Balouet & Buffetaut, 1987
† <i>Mekosuchus kalpokasi</i> Mead <i>et al.</i> , 2002
† <i>Mekosuchus sanderi</i> Willis, 2001
† <i>Mekosuchus whitehunterensis</i> Willis, 1997a
† <i>Paludirex gracilis</i> (Willis & Molnar, 1997a) Ristevski <i>et al.</i> , 2020a
=† <i>Pallimnarchus gracilis</i> Willis & Molnar, 1997a
† <i>Paludirex vincenti</i> Ristevski <i>et al.</i> , 2020a
† <i>Quinkana babarra</i> Willis & Mackness, 1996
† <i>Quinkana fortirostrum</i> Molnar, 1982c
† <i>Quinkana meboldi</i> Willis, 1997a
† <i>Quinkana timara</i> Megirian, 1994
† <i>Trilophosuchus rackhami</i> Willis, 1993b
† <i>Volia athollandersoni</i> Molnar <i>et al.</i> , 2002
CROCODYLIDAE (Cuvier, 1807)
<i>Crocodylus halli</i> Murray <i>et al.</i> , 2019
<i>Crocodylus johnstoni</i> (Krefft, 1873)
<i>Crocodylus novaeguineae</i> (Schmidt, 1928)
<i>Crocodylus porosus</i> Schneider, 1801
=† <i>Crocodylus nathani</i> Longman, 1924
CROCODYLIFORM ICHNOTAXA
† <i>Hatcherichnus</i> ichnosp. indet. Foster & Lockley, 1997 (Poropat <i>et al.</i> , 2021)

Revised from Thorn *et al.* (2021b). Note *Isisfordia molnari* may be a junior synonym of *Isisfordia selaslophensis* (see Hart 2020); placement of Mekosuchinae within Longirostres and as a subclade of Crocodyloidea is uncertain; placement of *Kalthifrons aurivellensis* outside of Mekosuchini is tentative; ‘*Baru*’ *huberi* is not referable to the genus *Baru* (see Yates 2017, Lee & Yates 2018); *Ultrastenos willisi* requires revision; ‘*Gavialis papuensis*’ requires revision; *Crocodylus nathani* requires revision; taxonomic validity of *Crocodylus halli* is based on morphometric data.

Table 2. List of all currently named crocodyliform species from Australasia.

Taxon	Age	Locality/Distribution	Source
<i>Australosuchus clarkae</i>	Chattian, late Oligocene	Etadunna Formation, Lake Eyre Basin, SA; Namba Formation, Lake Eyre Basin, SA	Willis & Molnar (1991b); Yates (2017)
' <i>Baru</i> ' <i>huberi</i>	Chattian, late Oligocene	White Hunter, Riversleigh WHA, QLD	Willis (1997a)
<i>Baru darrowi</i>	Langhian–middle Serravallian, Middle Miocene	Ringtail, Riversleigh WHA, QLD; Bullock Creek, Camfield station, NT	Willis <i>et al.</i> (1990); Yates (2017)
<i>Baru wickeni</i>	Chattian, late Oligocene	D Site and White Hunter, Riversleigh WHA, QLD	Willis (1997a); Yates (2017)
<i>Confractosuchus sauroktonos</i>	Cenomanian–early Turonian, Late Cretaceous	Winton Formation, Elderslie Station, QLD	White <i>et al.</i> (2022)
<i>Crocodylus halli</i>	present (no known fossil record)	southern New Guinea	Murray <i>et al.</i> (2019); extant
<i>Crocodylus johnstoni</i>	Late Pleistocene–present	Terrace Site, Riversleigh WHA, QLD (fossil); 'Leichhardt 3', Floraville Station, QLD (fossil); mainland northern Australia (QLD, NT, WA)	Willis & Archer (1990); Isberg <i>et al.</i> (2017); extant
<i>Crocodylus novaeguineae</i>	present (no known fossil record)	northern New Guinea	Solmu & Manolis (2019); extant
<i>Crocodylus porosus</i>	present (no unambiguous fossil record; see text)	northern Australia, New Guinea, Vanuatu, as well as a vast range in southeast Asia	Webb <i>et al.</i> (2021); extant
' <i>Gavialis papuensis</i> '	Pleistocene (presumed)	Busai, Muyua, PNG	de Vis (1905); Molnar (1982a)
<i>Gungamarandu maunala</i>	Pliocene or Pleistocene	Darling Downs, QLD	Ristevski <i>et al.</i> (2021)
<i>Harpacochampsia camfieldensis</i>	Langhian, Middle Miocene	Bullock Creek, Camfield Station, NT	Megirian <i>et al.</i> (1991)
<i>Isisfordia duncani</i>	late Albian, Early Cretaceous	Winton Formation, Isisford, QLD	Salisbury <i>et al.</i> (2006)
<i>Isisfordia molnari</i>	Cenomanian, Late Cretaceous	Griman Creek Formation, Lightning Ridge, NSW	Hart <i>et al.</i> (2019)
<i>Isisfordia selaslophensis</i>	Cenomanian, Late Cretaceous	Griman Creek Formation, Lightning Ridge, NSW	Etheridge (1917); Hart <i>et al.</i> (2019); Hart (2020)
<i>Kalthifrons aurivellensis</i>	Pliocene	Golden Fleece, Lake Palankarina, SA	Yates & Pledge (2017)
<i>Kambara implexidens</i>	Ypresian, early Eocene	Tingamarra Station, near Murgon, QLD	Salisbury & Willis (1996)
<i>Kambara molnari</i>	middle Eocene–late Eocene	Stuart Deposit, The Narrows Graben, Gladstone QLD	Holt <i>et al.</i> (2005)
<i>Kambara murgonensis</i>	Ypresian, early Eocene	Tingamarra Station, near Murgon, QLD	Willis <i>et al.</i> (1993)
<i>Kambara taraina</i>	middle Eocene–late Eocene	Stuart Deposit, The Narrows Graben, Gladstone QLD	Buchanan (2009)
<i>Mekosuchus inexpectatus</i>	Late Pleistocene–Holocene	Pindai Caves, Grande Terre, New Caledonia; Kanumera, Ile des Pins, New Caledonia	Balouet & Buffetaut (1987)
<i>Mekosuchus kalpokasi</i>	Holocene	Arapus archaeological Site, Efate Island, Vanuatu	Mead <i>et al.</i> (2002)
<i>Mekosuchus sanderi</i>	late Langhian–middle Serravallian Middle Miocene	Ringtail, Riversleigh WHA, QLD	Willis (2001)
<i>Mekosuchus whitehunterensis</i>	Chattian, late Oligocene	White Hunter, Riversleigh WHA, QLD	Willis (1997a)
<i>Paludirex gracilis</i>	Late Pleistocene	Terrace Site, Riversleigh WHA, QLD	Willis & Molnar (1997a); Ristevski <i>et al.</i> (2020a)
<i>Paludirex vincenti</i>	mid-Pliocene–Pleistocene	Darling Downs and Lansdowne, QLD	Ristevski <i>et al.</i> (2020a); this study
<i>Quinkana babarra</i>	mid-Pliocene	Allingham Formation, Bluff Downs, QLD	Willis & Mackness (1996)
<i>Quinkana fortirostrum</i>	Middle Pleistocene	Tea Tree Cave, near Chillagoe, QLD	Molnar (1982c)
<i>Quinkana meboldi</i>	Chattian, late Oligocene	White Hunter, Riversleigh WHA, QLD	Willis (1997a)
<i>Quinkana timara</i>	Langhian, Middle Miocene	Bullock Creek, Camfield Station, NT	Megirian (1994)
<i>Trilophosuchus rackhami</i>	late Langhian–middle Serravallian, Middle Miocene	Ringtail, Riversleigh WHA, QLD	Willis (1993b); Ristevski <i>et al.</i> (2023)
<i>Ultratenos willisi</i>	Chattian, late Oligocene	Low Lion, Riversleigh WHA, QLD	Stein <i>et al.</i> (2016)
<i>Volia athollandersoni</i>	Late Pleistocene–Holocene	Voli Voli Cave and Wainibuku Cave, Viti Levu, Fiji	Molnar <i>et al.</i> (2002)

Junior synonyms or *nomina dubia* (*Crocodylus nathani*, *Pallimnarchus*) are not listed. Abbreviations: NSW, New South Wales; NT, Northern Territory; PNG, Papua New Guinea; QLD, Queensland; SA, South Australia; WA, Western Australia; WHA, World Heritage Area.

presented in Ristevski *et al.* (2020a, 2020b, 2021). The matrix consists of 257 morphological characters and 151 operational taxonomic units (OTUs). The difference between this version of the matrix and the one from Ristevski *et al.* (2023) is the inclusion of four additional taxa: '*Baru*' *huberi* Willis, 1997a, *Confractosuchus sauroktonos*, *Mekosuchus inexpectatus*, and *Volia athollandersoni*. The same morphological characters from Ristevski *et al.* (2023) were used here as well. The goniopholidid crocodyliform *Anteophthalmosuchus epikrator* Ristevski, Young, de Andrade & Hastings, 2018 served as an outgroup taxon. The

phylogenetic analyses were carried out in TNT v1.5 Willi Hennig Society Edition (Goloboff *et al.* 2008, Goloboff & Catalano 2016). As in Ristevski *et al.* (2023), eight separate analyses were conducted. The first set of four analyses was performed by using the traditional search option (TrS), while the other set of four analyses used the New Technology search option (NTS). In each set, one analysis was run under a 'traditional' equal weighting (EW) principal search methodology, whereas the other three analyses used the implied weighting (IW) methodology (Goloboff 1993). In the analyses that utilized the IW method, the *k* (concavity

constant) values were set to 5.0 ($k=5$), 12.0 ($k=12$), and 25.0 ($k=25$). In all analyses, 23 out of the 257 characters were treated as ordered (characters 21, 39, 49, 50, 54, 55, 82, 104, 118, 125, 142, 148, 149, 157, 159, 174, 200, 202, 221, 222, 239, 248 and 256). For most analyses, the program was set to 900 Mb of RAM with the maximum number of held trees being 99,999. An exception was made for the analysis performed with the TrS option and no IW, where the program was set to 1200 Mb of RAM and the maximum number of held trees was 180,000.

For the analyses performed with the TrS option, the settings used one random seed and 1000 replicates of Wagner trees, and the tree bisection reconnection (TBR) swapping algorithm saved 10 trees per replication. For one analysis, run under the TrS option and using no IW, TNT reported that some replications overflowed after the end of the initial search. Therefore, we performed a subsequent round of TBR with trees from RAM. As for the analyses performed under the NTS option, the same search protocols as in Ristevski *et al.* (2020a, 2021, 2023) were used here as well. The parameters applied in these analyses follow Young *et al.* (2016), which implement the new technology searches (sectorial search, ratchet, drift and tree fusion) set to 1000 random addition sequences (RAS). For the sectorial search, the selection size above 75 used 1000 drifting cycles, 1000 starts below 75 and trees were fused 1000 times. Additionally, the consensus sectorial search (CSS) and exclusive sectorial search (XSS) were set to 1000 rounds. For ratchet, the parameters were set to stop the perturbation phase when 1000 substitutions were made, or 99% of the swapping was completed and a total of 1000 iterations. For drift, the perturbation phase stopped when 1000 substitutions were made, or 99% of the swapping was completed, and the number of cycles was set to 1000. No changes were made to the tree fusion settings which were left at the default three rounds.

Node support was assessed by conducting Bremer and bootstrap analyses in TNT v1.5. The Bremer support was performed by running the script 'BREMER.RUN' and used the default settings. The bootstrap analysis (Efron 1979, Felsenstein 1985) was set to 1000 replicates, showing values of 50% and above. Two homoplasy metrics, the consistency index (CI; Kluge & Farris 1969) and retention index (RI; Farris 1989), were calculated by running the script 'STATS.RUN' in TNT v1.5.

Additional information on the taxon matrix and character dataset are given in the [Supplemental Data S2](#), with the NEXUS format in [Supplemental Data S3](#), and phylogenetic TNT format results in [Supplemental Data S4](#).

Institutional abbreviations

AM, Australian Museum (F, fossil), Sydney, Australia. **AAOD**, Australian Age of Dinosaurs Museum of Natural History (F, fossil), Winton, Australia. **CMC**, Chinchilla Museum Collection, Chinchilla, Australia. **GPIT**, Geological-Paleontological Institute of the Eberhard Karls University of Tübingen, Germany. **NMNZ**, Museum of New Zealand Te

Papa Tongarewa, Wellington, New Zealand. **NHMUK**, The Natural History Museum (OR, old register), London, UK. **NTM**, Museum and Art Gallery of the Northern Territory (P, palaeontology), Darwin and Alice Springs, Australia. **OU**, University of Otago, Dunedin, New Zealand. **QM**, Queensland Museum (F, fossil), Brisbane, Australia. **SAMA**, South Australian Museum (P, palaeontology), Adelaide, Australia. **TMM**, Texas Memorial Museum, Austin, USA. **UF**, University of Florida Museum of Natural History, Gainesville, USA. **UQ**, The University of Queensland (F, fossil), Brisbane, Australia. **UQSSAL**, Salisbury Collection, The University of Queensland, Brisbane, Australia.

Review of crocodyliform taxa from Australasia

Mesozoic taxa

Confractosuchus

Confractosuchus sauroktonos is a recently named taxon known from the partial remains of one individual (White *et al.* 2022). The specimen was discovered at Elderslie Station, central-western Queensland, upper Winton Formation (Cenomanian), ~93 Ma (Cook *et al.* 2013, Tucker *et al.* 2013, 2017). The holotype (Fig. 5) consists of a nearly complete skull and mandibles with dentition, and a semi-articulated postcranial skeleton missing the tail and hind limbs. The specimen was mostly decayed prior to burial as evidenced by the haphazard dispersal of its osteoderms throughout the skeletal remains. The majority of the forearms are preserved, with only slight disarticulation occurring mostly within the manual elements (White *et al.* 2022). The relative completeness of the skull enabled White *et al.* (2022) to conduct a geometric morphometric analysis, which found *Co. sauroktonos* to be a macro-generalist predator. This analysis was supported with the preservation of its stomach contents which were identified as belonging to a juvenile ornithomimid dinosaur. The lack of acid etching revealed the stomach contents had not long been digested following its demise, that is assuming that it possessed the highly acidic gut characteristic of living crocodylians (e.g., Cott 1961, Fisher 1981). Nevertheless, the stomach contents revealed similarities of feeding behaviour with extant crocodylians, with evidence of oral processing (tooth mark) and prey reduction (articulated vertebrae) (Njau & Blumenshine 2006).

The phylogenetic analyses by White *et al.* (2022) recovered *Co. sauroktonos* in a basal position within Eusuchia, although nodal support was weak. The position and construction of the secondary choana in *Co. sauroktonos* indicates that anteriorly it is bound by the palatines, which is unlike the typical eusuchian condition where the choana is entirely bound by the pterygoids (Huxley 1875). Moreover, the vertebral morphology of *Co. sauroktonos* is represented by both procoelous and amphicoelous vertebrae.

Isisfordia

Well-preserved and largely complete crocodyliform fossils from the Mesozoic of Australasia are a rarity. The best-

50 mm



Figure 5. *Confractosuchus sauroktonos*, AODF0890, holotype skull in left lateral view.

preserved and most complete material of a crocodyliform from Australia belongs to *Isisfordia duncani*. *Isisfordia duncani* is known from several specimens, including an almost complete articulated skeleton as well as a skull lacking the mandibles, recovered near Isisford in central-western Queensland. The holotype (a mostly complete articulated skeleton; Fig. 6A) is interpreted to be of an adult animal (Salisbury *et al.* 2006, Syme & Salisbury 2018), with some of the additional specimens interpreted as probable adults, as well as an adult/sub-adult and a juvenile specimen (Syme & Salisbury 2018). The original material derives from the Early Cretaceous (Albian) part of the Winton Formation, assigned a maximum age of 102.2–100.5 Ma based on U–Pb isotope dating of detrital zircons (Tucker *et al.* 2013). *Isisfordia duncani* was a relatively small-sized crocodyliform with an estimated TL of about 1.1 metres (Salisbury *et al.* 2006), and has a proportionally broad and flat snout (Fig. 6B). The taphonomy of *I. duncani* specimens was studied in detail by Syme & Salisbury (2018), where they concluded that *I. duncani* inhabited deltaic environments and was a brackish water-tolerant crocodyliform.

Following the description of *I. duncani*, two additional species of *Isisfordia* have been identified, both from the Cenomanian-aged Griman Creek Formation, which outcrops near the town of Lightning Ridge, New South Wales (Bell *et al.* 2019), about 800 km southeast of the *I. duncani* type locality. *Isisfordia molnari* is represented by a partial braincase (Fig. 6C) and was roughly the same size as *I. duncani* (Hart *et al.*, 2019). The holotype of *Isisfordia selaslophensis* (a maxillary fragment bearing teeth; Fig. 6D) was initially named *Crocodylus (Bottosaurus) selaslophensis* (Etheridge, 1917, spelling emended by Molnar 1980). Subsequent studies (Molnar 1980, Mannion *et al.* 2015 *supp. info*) cast doubt on this designation, as the holotype specimen clearly did not bear features warranting placement in either *Crocodylus* or *Bottosaurus* Agassiz, 1849. Hart *et al.* (2019) recognized similarities (particularly a posterior maxillary alveolar groove) between the ‘*selaslophensis*’ holotype and *I. duncani*, and

subsequently referred the specimen to *I. molnari*. However, despite the taxon’s *nomen dubium* status, the specific epithet ‘*selaslophensis*’ remained valid, thus Hart (2020) instated *Isisfordia selaslophensis*, and proposed that *I. molnari* is a junior subjective synonym of this taxon. This taxonomic hypothesis will only be confirmed following the discovery of overlapping material. The holotypic maxillary fragment of *I. selaslophensis* indicates a larger-bodied taxon than *I. duncani* and *I. molnari*, with more robust teeth.

Hart *et al.* (2021) described new material (including an associated vertebral series), and reappraised previously described crocodyliform fossils from the Griman Creek Formation, including those discussed by Molnar (1980) and Molnar & Willis (2001). Hart *et al.* (2021) concluded that all of this material was likely to pertain to a single taxon, *Isisfordia* sp. cf. *I. selaslophensis*.

Since its initial description, the phylogenetic affinity of *I. duncani* and the interpretation of its morphology have been a matter of debate. When first subjected to a phylogenetic analysis by Salisbury *et al.* (2006), *I. duncani* was recovered as the basal-most eusuchian. As such, *I. duncani* was originally interpreted as a transitional form between non-eusuchian neosuchians and crocodylian eusuchians based on several morphological features in the cranium and post-cranium (Salisbury *et al.* 2006). Eusuchian crocodyliforms are characterized by the possession of a certain combination of morphological traits, most notably secondary choanae that are anterolaterally bound by the pterygoids, and procoelous vertebrae (Huxley 1875). In their diagnostic revision of Eusuchia, Salisbury *et al.* (2006) added the sagittal segmentation of the paravertebral osteoderms as another distinguishing trait of the clade. It should be noted that the aforementioned morphological features are also found in some non-eusuchian crocodyliforms; however, their combined presence is yet unknown outside of Eusuchia (e.g., Salisbury *et al.* 2006, Turner & Pritchard 2015). Salisbury *et al.* (2006) interpreted the secondary choanae of *I. duncani* as being anterolaterally bound by the pterygoids, typical of

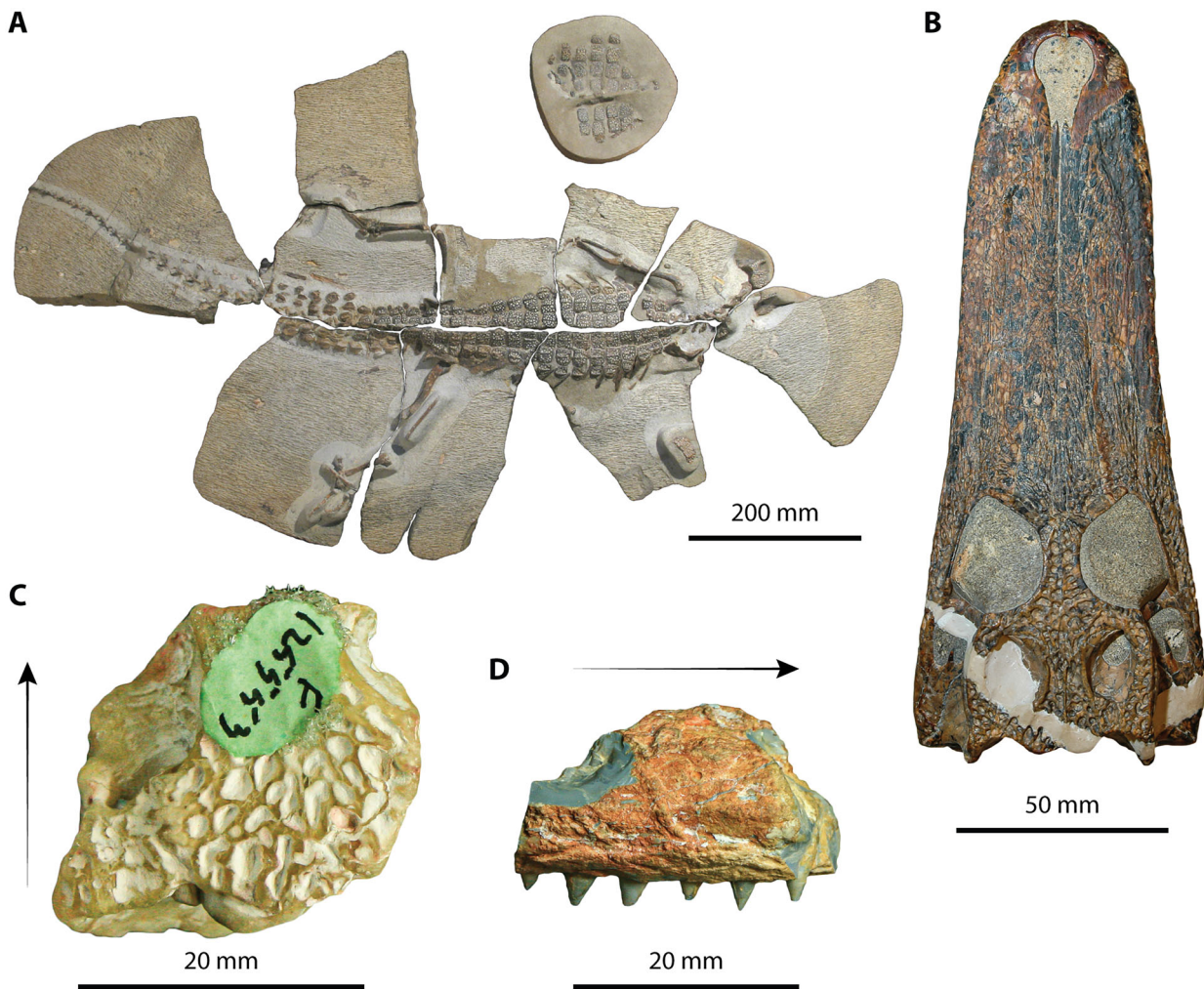


Figure 6. *Isisfordia*. **A**, *Isisfordia duncani*, QMF36211, holotype, skeleton in dorsal view. **B**, *Isisfordia duncani*, QMF44320, skull in dorsal view. **C**, *Isisfordia molnari*, AM F125553, holotype, partial cranium in dorsal view. **D**, *Isisfordia selaslophensis*, AM F15818, holotype, right maxillary fragment in lateral view. Arrows in C and D indicate anterior.

eusuchians. Additionally, the vertebrae of *I. duncani* were found to be incipiently procoelous, having a morphology somewhat intermediate between the amphicoelous condition of non-eusuchian crocodyliforms and the distinctly procoelous ones of eusuchians (Salisbury *et al.* 2006, Turner & Pritchard 2015, Hart *et al.* 2021). Further, *I. duncani* and eusuchians display sagittal segmentation of the paravertebral osteoderms, contrasting with the usually biserial paravertebral osteoderm configuration of non-eusuchian crocodyliforms (Salisbury *et al.* 2006). However, not all phylogenetic analyses have recovered *I. duncani* as a eusuchian. Pol *et al.* (2009) recovered two alternative positions for *I. duncani*, one congruent with the results by Salisbury *et al.* (2006), and a second where *I. duncani* formed a clade with the advanced neosuchians *Rugosuchus* Wu, Cheng & Russell, 2001 and *Shamosuchus* Mook, 1924. Other subsequent analyses have recovered *Isisfordia* as the sister taxon to *Susisuchus* Salisbury, Frey, Martill & Buchy, 2003, together comprising Susisuchidae (e.g., De Andrade *et al.* 2011, Turner 2015, Turner & Pritchard 2015, Young *et al.* 2016, Leite & Fortier 2018, Ristevski *et al.* 2020a, 2021, 2023, White *et al.* 2022, this study). Susisuchidae was erected for the late Early Cretaceous (Aptian) South American taxon

Susisuchus anatoceps Salisbury, Frey, Martill & Buchy, 2003, which was originally considered to be a non-eusuchian neosuchian clade. While *I. duncani* was yet to be formally described by the time of establishment for Susisuchidae, the possibility that ‘the Winton crocodylian’ (later named *Isisfordia*) could be a susisuchid was considered by Salisbury *et al.* (2003). In some studies, Susisuchidae was recovered as the sister clade to Eusuchia to the exclusion of *Isisfordia*, which was placed as the basal-most eusuchian (e.g., Fortier & Schultz 2009), or included in basal Eusuchia with *Susisuchus* (e.g., Andrade *et al.* 2011). An examination of *I. duncani* specimens by Turner & Pritchard (2015) suggested that the contact between the palatines and pterygoids is poorly preserved in the paratype skull of *I. duncani*, thus hampering confident assessment of the palatal morphology. Nonetheless, Turner & Pritchard (2015) stated that in *I. duncani*, it is the palatines that form the anterior boundaries of the secondary choanae and not the pterygoids, as is common among advanced neosuchians. As for the feeble procoely and tetraserial paravertebral osteoderms, it is known that they are also present in *Susisuchus* spp. (Salisbury *et al.* 2006, Figueiredo *et al.* 2011, Turner & Pritchard 2015, Leite & Fortier 2018). Therefore, some of the more recent

phylogenetic analyses found *Isisfordia* to be closely related to *Susisuchus* within Neosuchia, but outside of Eusuchia (e.g., Turner 2015, Turner & Pritchard 2015, Young *et al.* 2016, Rio & Mannion 2021). Nevertheless, support for eusuchian affinities of *Isisfordia* was presented by Leite & Fortier (2018), where they recovered Susisuchidae as a eusuchian sub-clade. In their description of the palatal morphology of *S. anatoceps*, Leite & Fortier (2018) pointed out that the secondary choanae of *Susisuchus* are completely enclosed by the pterygoids, similar to what was initially proposed for *I. duncani* by Salisbury *et al.* (2006). While this condition in *S. anatoceps* was still viewed as different from that of *I. duncani*, all phylogenetic analyses performed by Leite & Fortier (2018) recovered *Isisfordia* as a eusuchian within Susisuchidae.

Cenozoic taxa

Mekosuchinae

Australosuchus

The only recognized species of the genus *Australosuchus*, *Australosuchus clarkae*, is known from relatively abundant remains, including cranial and postcranial elements, found at several localities in South Australia (Willis & Molnar 1991b; see also Ristevski *et al.* 2020b and the supplementary files in Ristevski *et al.* 2023). The holotype specimen (Fig. 7) is a mostly complete, but rather poorly preserved, skull and mandible, and a partial postcranial skeleton from the late Oligocene–Early Miocene Etadunna Formation. All known specimens are considered to be late Oligocene–Early Miocene in age (Willis & Molnar 1991b, Willis 1997b). Three specimens referred to *A. clarkae* were discovered at Mampuwordu Sands, Lake Palankarina, which is dated as Late Pliocene–Early Pleistocene in age; however, these specimens are thought to have been reworked from the older Etadunna Formation and do not indicate the presence of this mekosuchine in younger deposits (Willis & Molnar 1991b, Willis 1997b). *Australosuchus clarkae* has been interpreted as a freshwater ‘generalist’ crocodylian (Willis & Molnar 1991a, Willis 1997a). The southern-most fossil

remains of *A. clarkae* are known from the Namba Formation at Lake Pinpa, which are Oligocene in age, and suggest that *A. clarkae* may have been a cold-tolerant species due to the far southern latitude and the relatively cool Australian climate during the Oligocene (Yates 2017).

Baru

Baru is a genus of large-bodied mekosuchines known from the Oligocene and Miocene of the Northern Territory and Queensland (Willis *et al.* 1990, Yates 2017). Currently, there are two named species of *Baru*: the type species *Baru darrowi* and *Baru wickeni* (Fig. 8). A third and as of yet unnamed species of *Baru* is known from the Late Miocene of Alcoota, Northern Territory (Yates 2017, see also Willis & Thomas 2005, Yates & Pledge 2017, and Lee & Yates 2018). The species ‘*Baru huberi*’ (Fig. 9) from the late Oligocene of the Riversleigh World Heritage Area (WHA) was originally assigned to *Baru* (Willis 1997a); however, a revision of the genus by Yates (2017) regarded ‘*Baru huberi*’ as sufficiently distinct to be referred to a different genus. That ‘*Baru huberi*’ is not referable to *Baru* was noted in the phylogenetic analyses by Lee & Yates (2018), and our results support this as well (read below). Species of *Baru* possess relatively long altirostral snouts and non-zipodont teeth. Another noteworthy feature is the loss of the second premaxillary tooth in small post-hatching *Baru* spp., resulting in five premaxillary alveoli early in ontogeny and four alveoli in more mature individuals (Willis *et al.* 1990, Willis 1997a, Yates 2017). However, this condition appears to be reversed in the unnamed *Baru* species from Alcoota (Yates 2017).

The oldest known species in this genus is *B. wickeni*, known from late Oligocene deposits in the Riversleigh WHA (Willis 1997a, 1997b, Yates 2017). Remains referred to *B. wickeni* were also reported from the Oligocene-aged Pwerte Marnte Marnte Local Fauna (abbreviated as LF here on) in the Northern Territory (Yates 2017; note that most of the Pwerte Marnte Marnte material is only tentatively referred to *B. wickeni*). The holotype of *B. wickeni* is a partially preserved rostrum and associated postcranial elements



200 mm

Figure 7. *Australosuchus clarkae*, QMF16788, holotype in dorsal view.

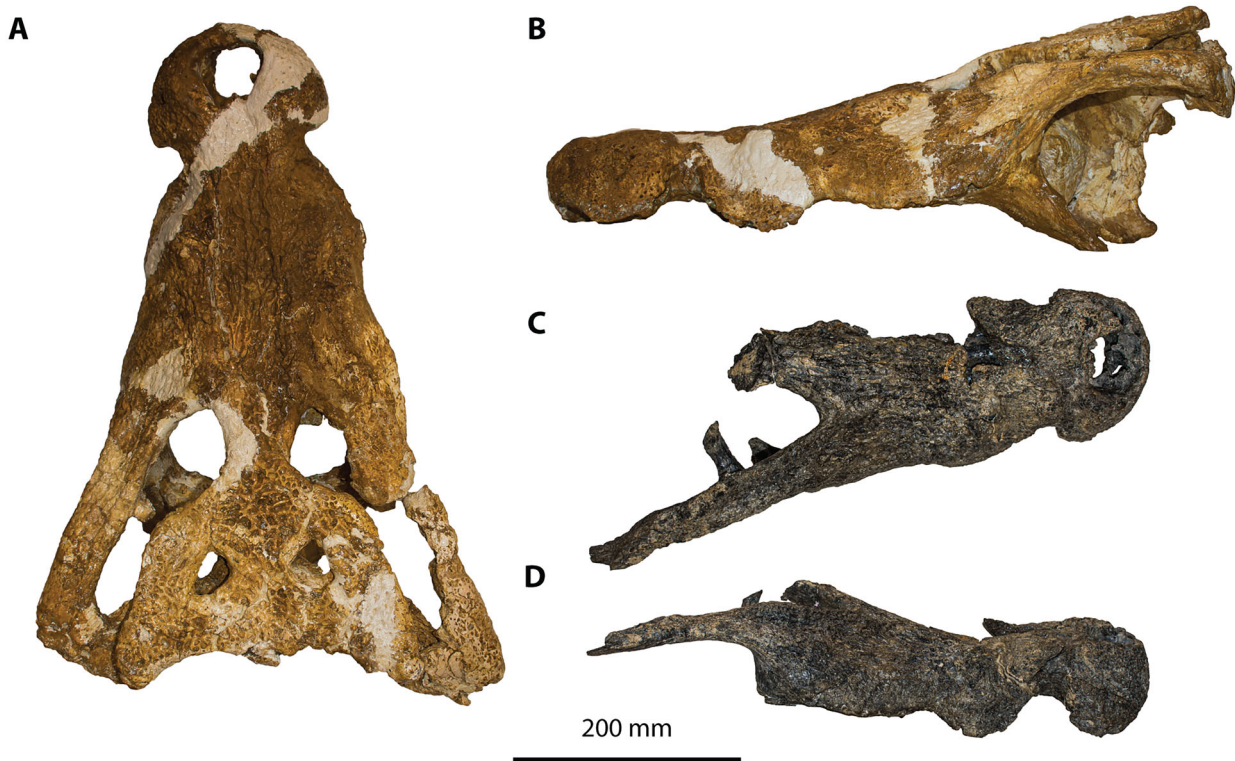


Figure 8. *Baru*. **A**, *Baru wickeni*, NTM P91171-1, skull in dorsal view. **B**, *Baru wickeni*, NTM P91171-1, skull in left lateral view. **C**, *Baru darrowi*, NTM P8695-8, holotype, partial skull in dorsal view. **D**, *Baru darrowi*, NTM P8695-8, holotype, partial skull in right lateral view.

(Willis 1997b, Yates 2017). Additional craniomandibular remains, including a nearly complete skull (NTM P91171-1) have also been referred to this taxon (Fig. 8A, B; Yates 2017). The type species, *B. darrowi*, is known from the Middle Miocene Bullock Creek LF and Ringtail Site from the Riversleigh WHA (Willis *et al.* 1990, Willis 1997a, Yates 2017). The holotype of *B. darrowi* (NTM P8695-8) is a relatively well-preserved rostral portion of the skull (Fig. 8C, D).

Based on the cranial morphology (such as the dorsally oriented external narial fenestra) and the fluvio-lacustrine sediments from where *Baru* spp. fossils have been recovered, species of *Baru* have been interpreted as semi-aquatic ambush predators capable of taking down large prey due to their robust skulls and teeth, and overall size (Willis *et al.* 1990, Megirian *et al.* 1991, Yates 2017). Numerous fossils, such as bird bones, from the Bullock Creek LF and the Hiatus A LF at Riversleigh bear bite marks that may have been inflicted by species of *Baru* (Murray & Vickers-Rich 2004, Scanlon 2006a).

Kalthifrons

The genus *Kalthifrons* was erected by Yates & Pledge (2017) based on craniomandibular remains discovered at the Golden Fleece locality, Lake Palankarina in South Australia, which are presumed to be from the Early Pliocene Mampuwordu Sand Member of the Tirari Formation. This genus contains only one named species, *K. aurivellensis*. Isolated teeth, as well as osteoderms and vertebral fragments, have been tentatively referred to this taxon (Yates & Pledge 2017). *Kalthifrons aurivellensis* is characterized by a

sub-triangular skull (when observed from a dorsal aspect: Fig. 10), with a dorsoventrally flattened platyrostral snout (Yates & Pledge 2017). The alveolar processes of the maxillae in this species are relatively well developed. Overall, the skull of *K. aurivellensis* is typical of a ‘generalist’ crocodylian, which implies a potentially similar palaeoecology to that of some species of *Crocodylus* (Yates & Pledge, 2017). The frontal of *K. aurivellensis* bears a strikingly elongated anterior process (Yates & Pledge 2017; see also supplemental document S3 of Ristevski *et al.* 2023). Also, the prefrontal of *K. aurivellensis* possesses a flange that projects laterally within the orbit (see figure 6 of Yates & Pledge 2017). *Kalthifrons aurivellensis* is a possible candidate for a crocodylian that went extinct due to direct competition with a species of *Crocodylus* (Yates & Pledge, 2017). Remains of a currently unnamed species of *Crocodylus* are known from the succeeding Pliocene Pompapillina Member of the Tirari Formation (read below), whereas there is no indication of *K. aurivellensis* in this member. This, coupled with the comparable rostral morphology and potentially similar habits of *K. aurivellensis* to some species of *Crocodylus*, may indicate that the former went extinct through competitive exclusion with the then newly arrived *Crocodylus* sp. (Yates & Pledge 2017).

Kambara

Kambara is the oldest named crocodylian genus from the Australasian Cenozoic (Eocene). There are four species referred to this genus and all of them come from Queensland: *Ka. murgonensis*, *Ka. implexidens*, *Ka. molnari* and *Ka. taraina*. Species of *Kambara* are medium-sized

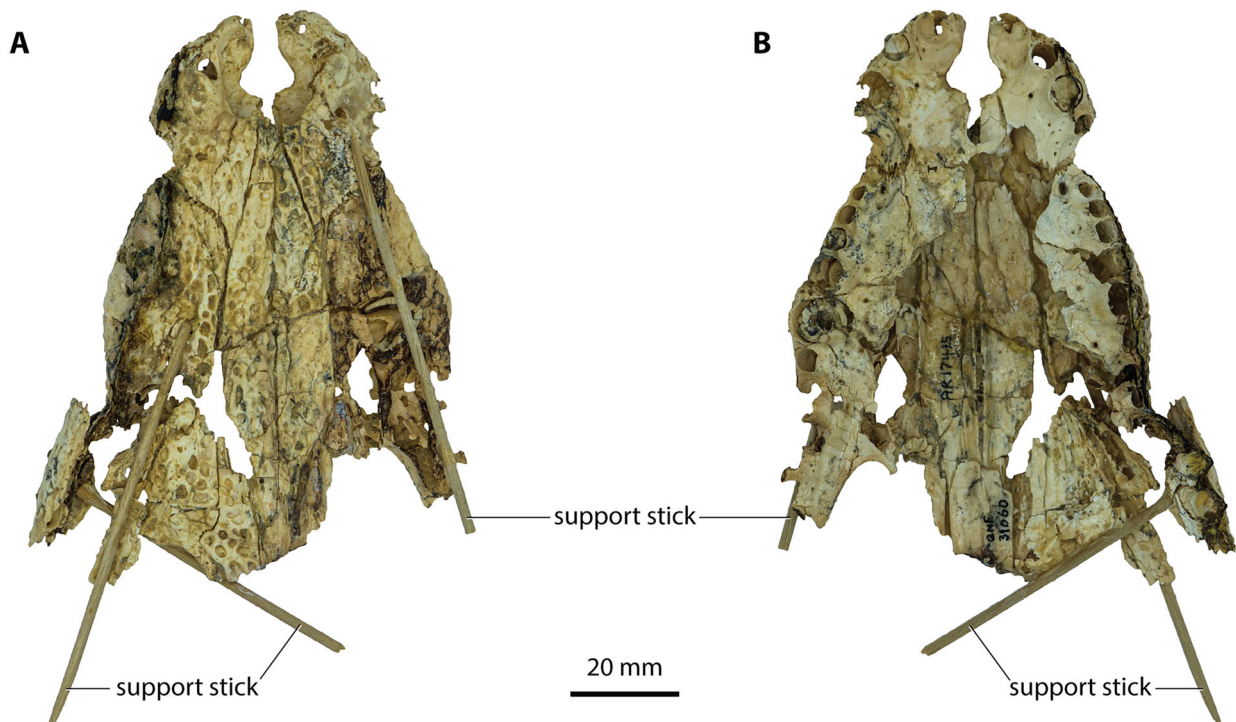


Figure 9. '*Baru' huberi*. QMF31060, holotype. A, Partial snout in dorsal view. B, Partial snout in ventral view.



Figure 10. *Kalthifrons aurivellensis*, SAMA P35062, holotype, skull in dorsal view.

crocodylians with moderately broad, platyrostral snouts, and non-serrate teeth (Willis *et al.* 1993, Salisbury & Willis 1996, Holt *et al.* 2005, Buchanan 2009). The type species, *Ka. murgonensis*, is from the early Eocene Tingamarra LF near the township of Murgon, in southeastern Queensland (Willis *et al.* 1993). Not long after the description of *Ka. murgonensis*, a second species, *Ka. implexidens* (Fig. 11A), was described by Salisbury & Willis (1996). Both *Ka. murgonensis* and *Ka. implexidens* are from the Tingamarra LF, which may imply sympatry between the two species. An alternative explanation was proposed by Salisbury & Willis (1996), who stated that instead of true sympatry, *Ka. murgonensis* and *Ka. implexidens* used the Murgon area as a nesting site, since hatchling-sized crocodylian remains and crocodylian eggshell fragments have also been recovered from the Tingamarra LF. *Kambara molnari* is the third described species of the genus. This species is slightly younger than the previous two species and derives from the mid-late Eocene Rundle Formation in eastern Queensland (Holt *et al.* 2005). Out of all *Kambara* species, *Ka. molnari* is the most poorly represented, with the holotype specimen being a partial left mandible (Fig. 11B; Holt *et al.* 2005, Coshell 1986, Ristevski *et al.* 2020b). Fragmentary postcranial material have also been referred to this taxon, albeit tentatively (Holt *et al.* 2005). Proportional differences in some of the dentary alveoli distinguish *Ka. molnari* from *Ka. murgonensis*, while the intermediate occlusal pattern of *Ka. molnari* differs from the overbite pattern of the type species and the interlocking ones of *Ka. implexidens* and *Ka. taraina* (Holt *et al.* 2005, Buchanan 2009). The fourth and latest named species of *Kambara* is *Ka. taraina* (Buchanan 2009, see also Buchanan 2008). So far, this species is the best represented of the genus *Kambara* and is known from plentiful cranial and



Figure 11. *Kambara*. A, *Kambara implexidens*, QMF29662, holotype, skull in dorsal view. B, *Kambara molnari*, QMF12364, holotype, left mandible in lateral view.

postcranial material (Buchanan 2008), although much of this material has never been formally published. While both *Ka. taraina* and *Ka. molnari* are from the Rundle Formation, Buchanan (2009) considered it unlikely that they were sympatric due to the stratigraphic separation within the formation from where the two species were recovered. Crocodylian bite marks, most likely inflicted by *Ka. taraina*, have been recorded on some turtle remains from the Rundle Formation (Buchanan 2008). Based on its postcranial morphology, Buchanan (2008) regarded *Ka. taraina* as a semi-aquatic ‘generalist’ predator. Pathologies such as fractures, infections, inflammations and possibly hemangioma on limb bones referred to *Ka. taraina* were also described by Buchanan (2008).

Mekosuchus

Australasia was once home to several small-bodied mekosuchines (TL of 2 m or less at maturity), some of them belonging to the genus *Mekosuchus* (see also *Trilophosuchus* below). *Mekosuchus inexpectatus* is the type mekosuchine taxon, which was named after craniomandibular and postcranial remains discovered in New Caledonia. Since the naming of *M. inexpectatus* in 1987, three other species have been assigned to the genus *Mekosuchus*: *M. kalpokasi*, *M. sanderi* and *M. whitehunterensis*. Beside their small sizes, species of *Mekosuchus* possess a suite of peculiar morphological features, such as anterolaterally oriented external nares; a short and deep snout; and, uniquely among eusuchians, maxillae that participate in the orbital margins (Fig. 12A; Balouet & Buffetaut 1987, Willis 1997b, 2001). Species of *Mekosuchus* from both mainland Australia and South West Pacific islands are small-sized taxa, which indicates

that the insular species of *Mekosuchus* did not evolve small body sizes as a consequence of island dwarfism (Brochu 2006, Ineich 2009).

The genus *Mekosuchus* has the longest known fossil record out of all Australasian crocodylians, spanning from the late Oligocene to the Holocene (Fig. 3). The oldest recognized species is *M. whitehunterensis* from the late Oligocene of the Riversleigh WHA, and is known primarily from craniomandibular remains (Fig. 12B, D, E; Willis 1997a; see also supplemental document S1 in Ristevski et al. 2020b). Additional cranial material and isolated postcranial elements have been tentatively referred to the species in the past (Holt & Salisbury 2005, Stein et al. 2015). *Mekosuchus sanderi* was discovered from the Middle Miocene Ringtail Site of the Riversleigh WHA (Fig. 12A, C; Willis 2001, see also supplemental document S1 of Ristevski et al. 2020b, 2023). It is thus far represented by fragmentary cranial remains, including a partial but well-preserved cranial table (Fig. 12C; Willis 2001, Ristevski et al. 2020b, Ristevski et al. 2023). Like *M. inexpectatus* and *M. whitehunterensis*, the orbital margins of the frontal in *M. sanderi* are broad and convex (Fig. 12C, D; Balouet 1991, Willis 1997a, Ristevski et al. 2020b). *Mekosuchus inexpectatus* is known from multiple specimens (e.g., Fig. 13A; Balouet 1991), most of which are undescribed. The first described New Caledonian material was dated to the Holocene (Balouet & Buffetaut 1987, Balouet 1989); however, a Late Pleistocene age has also been proposed (Willis 2006, Holt et al. 2007). Additional remains of *M. inexpectatus* have been reported from archaeological sites in New Caledonia, which corroborates the Holocene survival of this species (Balouet 1991). *Mekosuchus inexpectatus* had a proportionally short and wide snout, proportionally large orbits, and tribodont dentition (small and bulbous

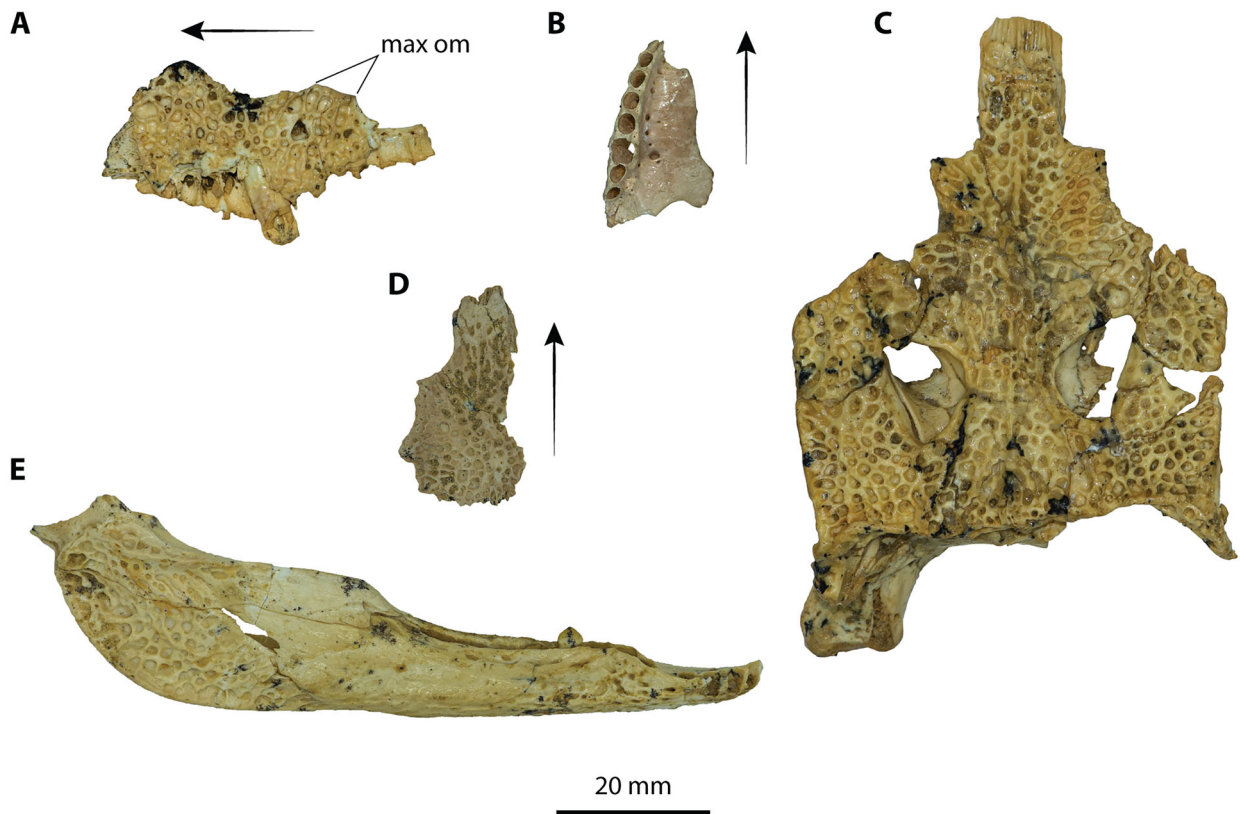


Figure 12. *Mekosuchus* from the Riversleigh World Heritage Area. **A**, *Mekosuchus sanderi*, QMF31188, holotype, partial left maxilla in lateral view. **B**, *Mekosuchus whitehunterensis*, QMF31051, holotype, partial right maxilla in ventral view. **C**, *Mekosuchus sanderi*, QMF31166, partial cranium in dorsal view. **D**, *Mekosuchus whitehunterensis*, QMF31052, partial frontal in dorsal view. **E**, *Mekosuchus whitehunterensis*, QMF31053, right mandible in lateral view. Arrows in A, B, and D indicate anterior. Abbreviation: max om, orbital margin of the maxilla.

posterior teeth used primarily for crushing). The latter feature may indicate that *M. inexpectatus* incorporated hard-shelled invertebrates into its diet, such as molluscs and crustaceans (Buffetaut 1983, Balouet & Buffetaut 1987, Balouet 1989, 1991, Flannery 1994). Balouet & Buffetaut (1987) and Balouet (1991) suggested a primarily terrestrial palaeoecology for *M. inexpectatus* based on the anterodorsal orientation of its nares, the snout shape, and morphology of the postcrania (see also Balouet 1989, Flannery 1994, Willis 1997b, 2006, Scanlon 2014). Holt *et al.* (2007) hypothesized that *M. inexpectatus* may have preferred slow-moving rainforest streams, foraged near the water edge as well as on land, and may have been nocturnal. Similar to Holt *et al.* (2007), Salisbury *et al.* (2010) hypothesized that based on their anatomy, the species of *Mekosuchus* may have had comparable palaeoecologies and behaviour to extant species of *Paleosuchus* Gray, 1862 and *Osteolaemus* Cope, 1861. The other insular taxon that has been assigned to the genus *Mekosuchus* is *M. kalpokasi* from Vanuatu (Mead *et al.* 2002). The mekosuchine remains from Vanuatu are the youngest known, dated to around 3000 years B.P. (Mead *et al.* 2002). *Mekosuchus kalpokasi* is known mainly from a left maxilla, and as such it is more poorly represented than *M. inexpectatus*, *M. sanderi* and *M. whitehunterensis*, all known from comparatively more abundant material.

Anthropogenic factors may be to blame for the extinction of the insular species of *Mekosuchus*, as the disappearance of

these crocodylians along with other endemic fauna occurred not long after the arrival of humans on those Melanesian islands (Balouet 1984, 1989, 1991, Balouet & Buffetaut 1987, Chazeau 1993, Milberg & Tyrberg 1993, Flannery 1994, Mittermeier *et al.* 1996, Mead *et al.* 2002, Brochu 2003). However, some authors have stated that direct evidence for the insular mekosuchines being extirpated by humans is lacking (e.g., Anderson *et al.* 2010, Slavenko *et al.* 2016). The potentially human-caused extinction of species of *Mekosuchus* should be evaluated in future studies.

Paludirex

As mentioned above, the genus *Paludirex* was established for several specimens that were previously referred to ‘*Pallimnarchus*’ (see Ristevski *et al.* 2020a). There are two recognized species of *Paludirex*: the type species *P. vincenti*, and *P. gracilis*. *Paludirex vincenti* is the better represented of the two species. The holotype of *P. vincenti* is a partial skull (Fig. 14A, B) from the Pliocene of the Darling Downs (more specifically, the Chinchilla LF). Another specimen of *P. vincenti* (QMF11626) was also discovered in the Darling Downs region, although it is unclear if QMF11626 is Pliocene or Pleistocene in age (Ristevski *et al.* 2020a). Herein, we recognize a third specimen as probably referable to *P. vincenti*, QMF1752 (Fig. 14C–F). Specimen QMF1752, also known as the ‘Lansdowne snout’ (after the Lansdowne Station locality; Longman 1925), is an incomplete and

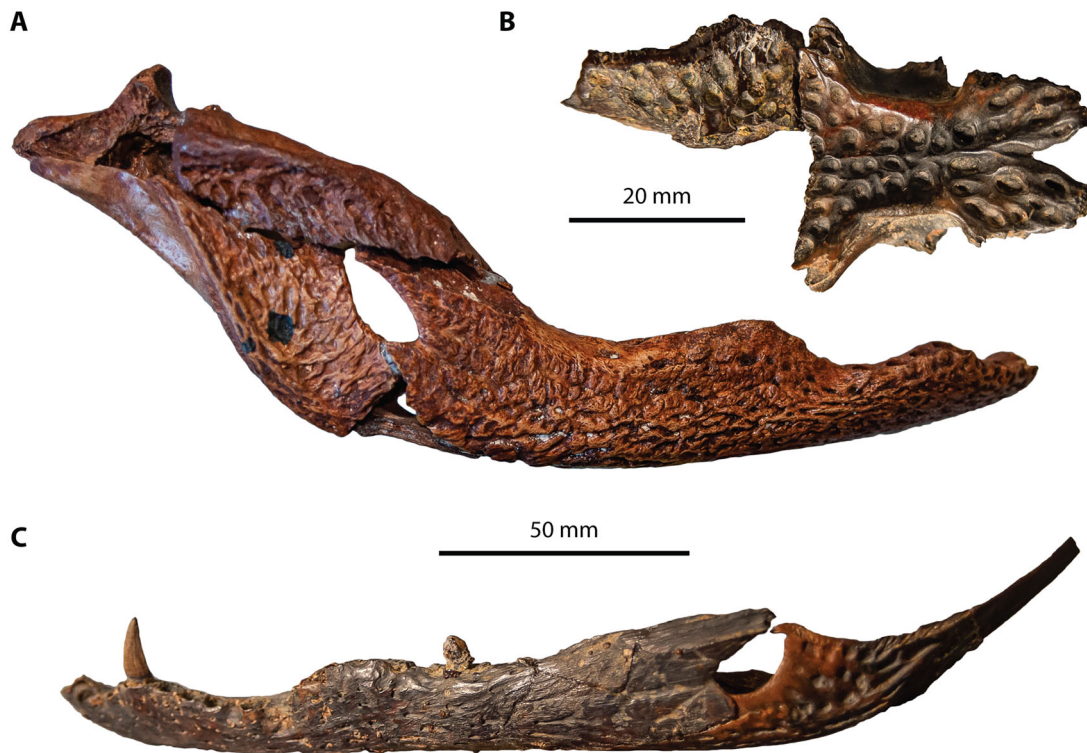


Figure 13. *Mekosuchus inexpectatus* and *Volia athollandersoni*. **A**, *Mekosuchus inexpectatus*, NCP 06, holotype, right mandible in lateral view. **B**, *Volia athollandersoni*, NMNZ S37341, holotype (frontal fragment), and NMNZ S37342 (parietal) in dorsal views. **C**, *V. athollandersoni*, NMNZ S37332, partial left mandible in lateral view.

slightly dorsoventrally compressed skull from the Middle or Late Pleistocene (the exact Pleistocene age of this specimen is uncertain) of Queensland that preserves almost the entirety of the cranial rostrum up to the orbital region. This specimen has had several taxonomic treatments in the last 98 years: originally as ‘*Pallimnarchus pollens*’, then *C. porosus*, followed by ‘*Pallimnarchus*’ sp., ‘*Pallimnarchus gracilis*’, and the most recent being *Crocodylia incertae sedis* (see Ristevski *et al.* 2020a for a detailed review). We were able to assess the morphology of this specimen using CT scan data and through limited observations as it was displayed at the Queensland Museum in Brisbane. From our observations, we conclude that QMF1752 is most likely referable to *P. vincenti* as its morphology is consistent with this species as diagnosed by Ristevski *et al.* (2020a). These features include: premaxillary depth that is ~47% the collective premaxillary width; the 1st premaxillary alveolus is positioned approximately medial to the 2nd, and these alveoli are separated from each other by an interalveolar gap; the 4th premaxillary alveolus is the largest and is almost twice the size of the 3rd alveolus; the external narial fenestra is subcircular, with a posterior margin that curves gently in a posteromedial direction; a substantial size disparity between the maxillary alveoli, with the 5th maxillary alveolus being significantly larger than the smallest interfenestral alveolus; and the teeth are conical and non-serrated.

Paludirex gracilis (formerly ‘*Pallimnarchus*’ *gracilis*) is known from few fragmentary rostromandibular remains discovered at Terrace Site, Riversleigh WHA, which has been dated to the Late Pleistocene (~50 ka; Davis & Archer 1997, Willis & Molnar 1997a, Woodhead *et al.* 2016, Ristevski

et al. 2020a). Based on currently known material, *P. gracilis* is distinguished from *P. vincenti* on the basis of its snout proportions, with *P. gracilis* having a proportionally less robust snout than *P. vincenti* (Ristevski *et al.*, 2020a). The two species of *Paludirex* are interpreted as semi-aquatic ambush predators capable of taking on relatively large prey (Ristevski *et al.* 2020a, Ristevski 2022b). *Paludirex gracilis* was one of the last surviving mekosuchines in Australia, and its extinction may be a consequence of climatic and environmental changes that occurred during the Late Pleistocene (Ristevski *et al.* 2020a).

Quinkana

Species of the genus *Quinkana* are some of the most distinctive mekosuchines, as they are characterized by an altirostral snout morphology, well-developed maxillary alveolar processes, and ziphodont dentition. This genus was named by Molnar (1982c), with the type species being *Q. fortirostrum*. Besides *Q. fortirostrum*, there are three other named species of *Quinkana*: *Q. babarra*, *Q. meboldi* and *Q. timara*. The genus *Quinkana* has a relatively long fossil record in Australia (late Oligocene–Pleistocene), with the oldest known species being *Q. meboldi* from the late Oligocene White Hunter Site (~25 Ma) in the Riversleigh WHA. *Quinkana meboldi* is known from several partially preserved craniomandibular and dental elements, with the holotype specimen being a nearly complete left maxilla (Fig. 15A). The preserved teeth in the specimens assigned to *Q. meboldi* are labiolingually compressed, but their carinae do not bear denticles (Willis 1997a). After *Q. meboldi*, the next oldest known species is *Q. timara* from the Middle–Late Miocene

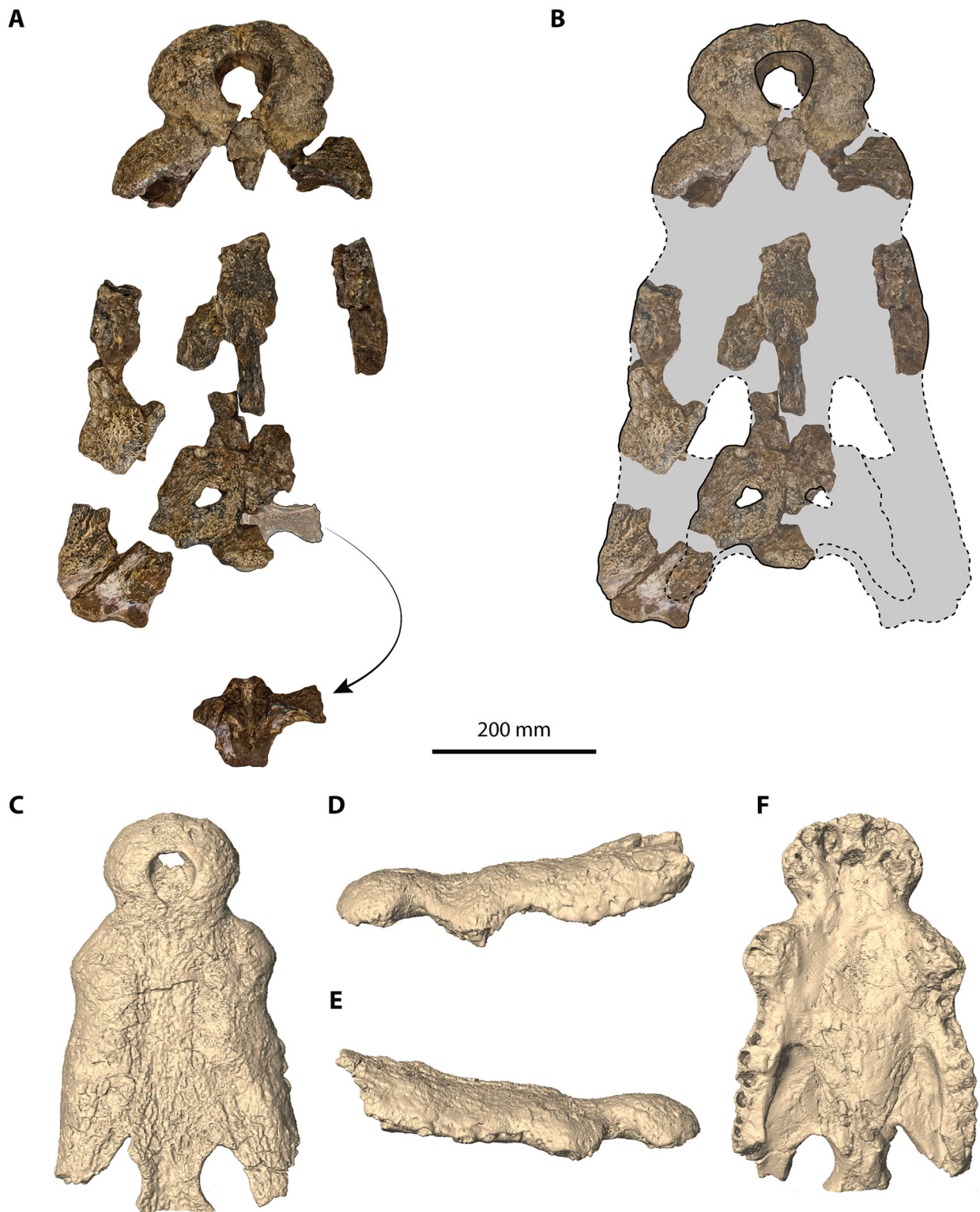


Figure 14. *Paludirex vincenti*. A, 'Geoff Vincent's specimen' (CMC2019-010 + QMF59017), holotype, partial skull, all skull pieces in dorsal view; arrow indicates basiocranium (QMF59017) ventral to the cranial table (CMC2019-010-5). B, Skull of 'Geoff Vincent's specimen' in dorsal view; dashed lines indicate hypothetical outline of the skull. QMF1752, digital model of the partial skull in C, dorsal, D, left lateral, E, right lateral, and F, ventral views. A and B are modified from Ristevski *et al.* (2020a).

of Bullock Creek (Fig. 15B; Megirian 1994). *Quinkana timara* is currently the best represented species of *Quinkana* and is known from several partially preserved craniomandibular elements, isolated teeth and other undescribed material (Megirian 1994, Yates & Pledge 2017). The teeth of *Q. timara* are ziphodont as they are labiolingually compressed

and bear well-developed denticles on their carinae (Megirian 1994). Known from the Early Pliocene Allingham Formation of northeastern Queensland is *Q. babarra*. *Quinkana babarra* was named on the basis of a right maxillary piece (Fig. 15C), and several isolated ziphodont teeth may also be attributable to this species (Willis & Mackness 1996).

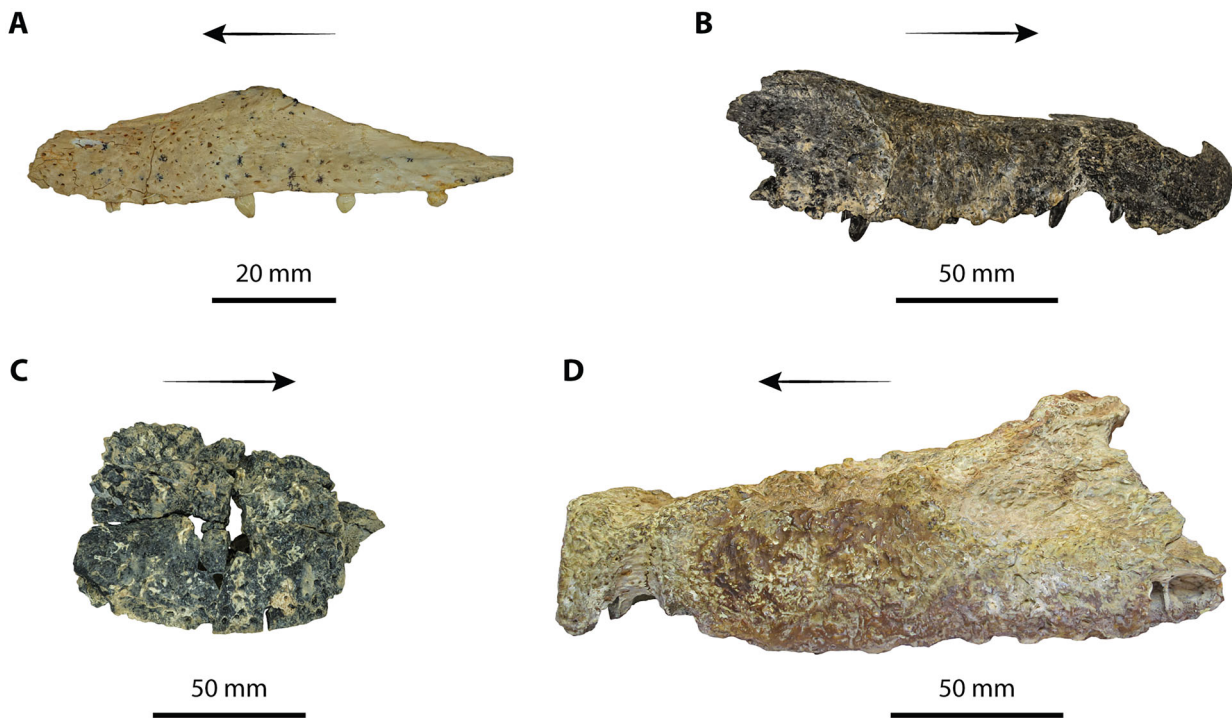


Figure 15. *Quinkana*. A, *Quinkana meboldi*, QMF31056, holotype, left maxilla in lateral view. B, *Quinkana timara*, NTM P895-19, holotype, partial snout in right lateral view. C, *Quinkana babarra*, QMF23220, holotype, right maxillary piece in lateral view. D, *Quinkana fortirostrum*, AM F57844, holotype, snout in left lateral view. Arrows indicate anterior.

Compared to the other species of *Quinkana*, *Q. babarra* is the least understood due to the fragmentary nature of its holotype and thus far the only specimen that is definitively referable to the species. The type species of *Quinkana*, *Q. fortirostrum*, is known from only a well-preserved snout (Fig. 15D). Although the alveoli of the *Q. fortirostrum* holotype are labiolingually compressed, there are no known teeth that are unequivocally attributable to this species. The external narial fenestra of *Q. fortirostrum* is oriented anterodorsally. An anterodorsally oriented external narial fenestra is also present in *Q. timara*, whereas this condition is unknown in *Q. meboldi* and *Q. babarra*. The holotype of *Q. fortirostrum* was discovered at Tea Tree Cave in northern Queensland, which is Middle Pleistocene in age (Molnar 1982c). The Middle Pleistocene age estimate for the *Q. fortirostrum* holotype is only presumed, as direct dating on the specimen itself has never been performed, although a Middle Pleistocene age has been determined for other material from Tea Tree Cave (Price *et al.* 2013). The holotype of *Q. fortirostrum* was first described by Molnar (1977), who recognized its distinctiveness, but at the time did not provide a formal taxonomic assignment. The same specimen was subsequently discussed by Molnar (1978a, b), and then classified as its own genus and species by Molnar (1982c). Because the currently described material of all four species of *Quinkana* are quite fragmentary and limited to incomplete craniomandibular elements, much of the anatomy of these species remains unknown.

Throughout the decades, many isolated and fragmentary remains of ziphodont crocodylians have been referred to the genus *Quinkana* (e.g., Molnar 1982c; Sobbe *et al.* 2013). However, much of this material should be reassessed in light

of evidence of a new ziphodont mekosuchine genus other than *Quinkana* ('Floraville taxon' in Fig. 3; Molnar *et al.* 2017, Price *et al.* 2019, Ristevski *et al.* 2019). Though all known material definitively referable to species of *Quinkana* comes from mainland Australia, isolated crocodyliform teeth from the Pliocene Otibanda Formation in Papua New Guinea reported by Plane (1967) may be possibly attributable to this genus (Willis 1997a; Molnar *et al.* 2002, Wroe 2002, Brochu 2003). The Papua New Guinea material mentioned by Plane (1967) has never been described or figured in detail, and we were unable to examine it for the purposes of this study. Therefore, the putative ziphodont teeth from Papua New Guinea should be studied in detail before determining if they can be referred to the genus *Quinkana* or perhaps a different taxon.

The palaeoecology of species of *Quinkana* has been a topic of interest, especially because of the notion that these species may have been better adapted for life and prey acquisition on land compared to extant crocodylians (Molnar 1982c, 2004, Flannery 1990, 1993, Willis *et al.* 1990, Megirian *et al.* 1991, Megirian 1994, Willis & Mackness 1996, Willis 1997a, Willis & Molnar 1997b, Murray & Vickers-Rich 2004, Scanlon 2014, Long 2017, Price *et al.* 2017, Stein *et al.* 2017, Yates & Pledge 2017). Willis *et al.* (1990) suggested that ziphodont crocodylians such as species of *Quinkana* may have subdued their prey in a manner similar to that of the Komodo dragon. While not specifically referring to *Quinkana* spp., a similar proposition was given by Busbey (1986, 1995), who argued that crocodyliforms with altirostral/orenirostral snouts and ziphodont dentition most likely acquired and manipulated their prey like terrestrial reptilian carnivores do, and unlike semi-aquatic

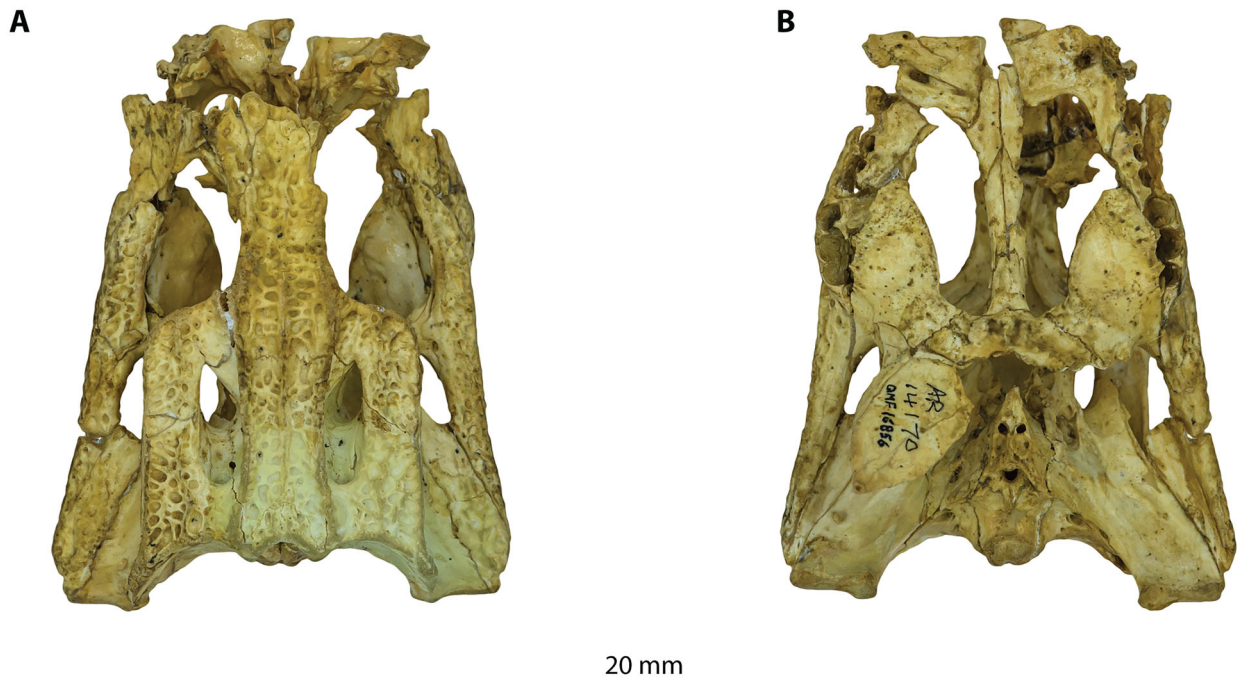


Figure 16. *Trilophosuchus rackhami*, QMF16856, holotype. A, Cranium in dorsal view. B, Cranium in ventral view.

crocodylians with platyrostral snouts. Others have hypothesized that while species of *Quinkana* probably had more terrestrial lifestyles and feeding habits compared to extant crocodylians, they were still dependent on water sources for thermoregulation, protection and reproduction (Willis 1997b; see also Mackness & Sutton 2000). However, not all have agreed with these proposals, such as Wroe (2002), who argued that based on the taphonomy and known material, there is insufficient evidence to support the suggestion of terrestriality in species of *Quinkana*. Further inferences on the palaeobiology of *Quinkana* spp. are currently limited by the scarce fossil remains attributable to these species.

While the genus *Quinkana* was recovered as a mekosuchine in our phylogenetic analyses, alternative taxonomic referrals have been proposed in the past, particularly with planocraniids (Rauhe & Rossmann 1995, Rossmann 1998, 1999) or as a non-mekosuchine crocodylid (Rio & Mannion 2021). However, a relationship between *Quinkana* spp. and Planocraniidae has not been supported by most phylogenetic analyses, and *Quinkana* is almost always recovered within Mekosuchini (e.g., Willis 1993b, Salisbury & Willis 1996, Molnar *et al.* 2002, Brochu 2001, 2003, 2007a, 2012, Buchanan 2008, Brochu & Storrs 2012, Stein *et al.* 2016, Yates & Pledge 2017, Lee & Yates 2018, Ristevski *et al.* 2020a, 2020b, 2021, 2023, Rio & Mannion 2021; see below).

Trilophosuchus

One of the most morphologically distinctive crocodylians from Australia is *Trilophosuchus rackhami*. This taxon was named after an incomplete but exceptionally well-preserved cranium that was discovered at the Middle Miocene Ringtail Site, Riversleigh WHA (Fig. 16; Willis 1993b, Ristevski 2022a, Ristevski *et al.* 2023). Additional isolated cranial

elements are also referable to this species (Willis 1993b, Ristevski *et al.* 2023). At present, only one species is recognized in the genus *Trilophosuchus*, *T. rackhami*. However, an isolated parietal from Hiatus Site at the Riversleigh WHA demonstrates the presence of the genus *Trilophosuchus* during the late Oligocene (Ristevski *et al.* 2023). *Trilophosuchus rackhami* is characterized by several striking morphological features, such as a cranial table that bears three continuous longitudinal crests (hence the generic name *Trilophosuchus*, meaning ‘three crested crocodile’), a relatively short but broad altirostral snout (inferred, as no complete snout is known for *T. rackhami*), and an overall small body-size at maturity (estimated TL of the holotype specimen QMF16856 is 70–90 cm; Ristevski *et al.* 2023). In addition, *T. rackhami* displays paedomorphic features such as a lateroventrally sloping cranial table, a basioccipital plate that is oriented posteroventrally, and a small body size at maturity. The maxilla, lacrimal and jugal of *T. rackhami* have a unique relationship around the orbit, where the maxilla is excluded from participating to the orbital margin by a narrow contact formed by the lacrimal and jugal (Ristevski *et al.* 2023). This morphology is intermediate between the common condition in most other crocodylians, where the lacrimal and jugal broadly separate the maxilla from the orbit, and that in *Mekosuchus* spp., where in the latter the maxilla participates in the orbit.

The neuroanatomy of *T. rackhami* was described in detail by Ristevski (2022a), who found that the brain endocast of the taxon resembles some notosuchian crocodyliforms, the common crus of the endosseous labyrinth is relatively tall, and that *T. rackhami* has a highly developed paratympanic pneumatic system that is most similar to, and even slightly greater than, the paratympanic pneumatic system of the extant *Paleosuchus palpebrosus* Cuvier, 1807 and

Osteolaemus tetraspis Cope, 1861. Based on its neuromorphology, Ristevski (2022c, 2022b) suggested that *T. rackhami* likely had a terrestrial palaeoecology and, when compared to extant crocodylians, probably had a palaeoecology most similar to those of *Pa. palpebrosus* and *O. tetraspis*. Furthermore, Ristevski (2022b, 2022c) hypothesized that, due to the highly developed paratympanic pneumatic system, as well as additional neuromorphological similarities of the brain endocast and endosseous labyrinth shared with certain basal crocodylomorphs, basal crocodyliforms and notosuchians, *T. rackhami* may have exhibited even greater terrestrial tendencies than any extant crocodylian. Willis (1993b) also proposed a terrestrial palaeoecology for *T. rackhami* based on its cranial morphology and its resemblance not only to *Pa. palpebrosus* and *O. tetraspis*, but also some notosuchians, atoposaurid neosuchians and basal crocodyliforms (see also Willis 1997b, 2006, Scanlon 2014).

Ultrastenos

The genus *Ultrastenos* was named from fragmentary material discovered at the late Oligocene Low Lion Site, Riversleigh WHA, and currently has one species assigned to it, *U. willisi*. *Ultrastenos willisi* was established on the basis of several craniomandibular and associated postcranial remains (Stein *et al.* 2016). During the late Oligocene, the environment of Low Lion Site, from where the holotype specimen of *U. willisi* originates, is indicative of an open forest lacking in river systems or large wetlands (Stein *et al.* 2016). In their phylogenetic analyses, Stein *et al.* (2016) found *U. willisi* within Mekosuchinae as a sister taxon to *T. rackhami*. More recently, *U. willisi* was incorporated as an OTU in the phylogenetic analyses by Rio & Mannion (2021), who recovered it in a polytomy with species of *Mekosuchus*. Stein *et al.* (2016) suggested that *U. willisi* may have had either a slender longirostrine or a proportionally short snout, although these interpretations are questionable and should be re-evaluated since much of the mandibular element assigned to this taxon is incomplete. New material of a related species indicates that significant revisions of this taxon are necessary (A. M. Yates, in prep.).

Volia

Another insular mekosuchine is *Volia athollandersoni* from the Quaternary of Fiji. *Volia athollandersoni* is known from fragmentary cranial and postcranial remains that were discovered in two caves on the island of Viti Levu, Fiji – the Wainibuku Cave, where the holotype specimen (Fig. 13B) was found, and the Voli Voli Cave (Molnar *et al.* 2002, see also Anderson 1999, Worthy & Anderson 1999, Worthy *et al.* 1999). The material is presumed to be Pleistocene in age; however, Molnar *et al.* (2002) did not exclude the possibility that the remains they described may be more recent. Based on the size, taphonomy, and the provenance of the preserved material, Molnar *et al.* (2002) deduced that the material they reported represents at least five individuals. Non-diagnostic, isolated crocodylian fragments from the Holocene of Naigani, Fiji have been tentatively referred to

the genus *Volia* (Irwin *et al.* 2011). Because of the lack of mammalian and other large reptilian predators, *V. athollandersoni* is regarded as a top predator from the Quaternary of Fiji, and some authors have suggested that it may have been primarily terrestrial (Anderson 1999, Worthy *et al.* 1999, Molnar *et al.* 2002). However, the fragmentary nature of the currently known material precludes confident palaeoecological inferences. In addition to the *V. athollandersoni* remains, the fossil assemblage from the Voli Voli Cave is composed of predominantly terrestrial species (birds, frogs, an iguana, snakes and possibly a tortoise; see Worthy *et al.* 1999, Molnar *et al.* 2002), some of which *V. athollandersoni* may have preyed on or scavenged (Molnar *et al.* 2002). Furthermore, based on the relatively small land mass of Fiji during the Pleistocene and Holocene, Molnar *et al.* (2002) postulated that the population of *V. athollandersoni* on the islands was also small.

Non-mekosuchine Cenozoic crocodylians

Crocodylus

Crocodylus is the most speciose genus of extant crocodylians globally, with 13 recognized species and a near-circumtropical distribution. Most species of *Crocodylus* have mesorostrine and platyrostral snouts, thus fitting within the ‘generalist’ ecomorphological category, although a couple of species have evolved the slender longirostrine ecomorph, including the Australian *C. johnstoni* (Figs 1A, 17C; Brochu 2001, Drumheller & Wilberg 2020). Non-*Crocodylus* crocodylids have a largely African distribution (Hekkala *et al.* 2021, Brochu *et al.* 2022), suggesting an ultimately African origin for the genus, although the crown group may have originated in the Indo-Pacific region (Oaks 2011). There are four extant species of *Crocodylus* living in Sahul (Australia and New Guinea; Figs 1, 17). *Crocodylus novaeguinae* (Fig. 17A) and *C. halli* (Fig. 17B) are endemic to New Guinea, *C. johnstoni* is endemic to Australia, while *C. porosus* (Figs 1B, 17D) occurs throughout the region and beyond into southeast Asia (Grigg & Kirshner 2015, Murray *et al.* 2019). Although this review is focused on the Australian continent, it should be noted that there is no confirmed fossil record of *Crocodylus* in New Guinea, although Plane (1967) suggested that postcranial elements from the Pliocene of New Guinea may be referable to *Crocodylus*.

Crocodylus does not appear in the Australian fossil record until the Early Pliocene epoch at ~4.5 Ma (Molnar 1979), presumably dispersing from Asia via ‘island hopping’ through southeast Asia and Wallacea (Willis 1997b). Based on the known fossil record, and the wider phylogenetic relationships of the extant Australian species, there were multiple waves of immigration and colonization of Australia. The earliest wave of immigration is poorly understood. A snout from a juvenile individual, initially identified as *C. porosus*, from the Pliocene Bluff Downs locality in Queensland is the most complete published specimen (Molnar 1979). The specific identification of this specimen has been questioned (Yates 2019) because it is not based on any autapomorphies or a unique combination of characters, and the snout shows proportional differences from modern

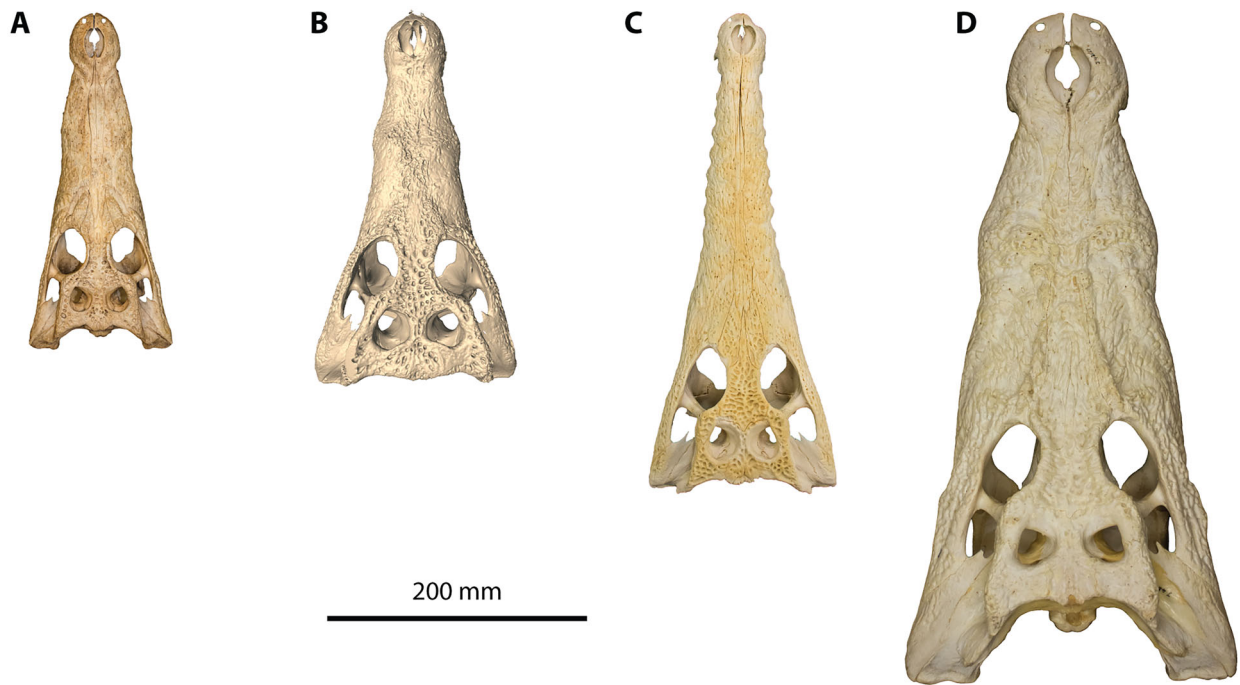


Figure 17. Skulls of extant *Crocodylus* from Australasia. **A**, *Crocodylus novaeguineae*, QMJ5332, skull in dorsal view. **B**, *Crocodylus halli*, UF 145927, digital model of the skull in dorsal view (downloaded from MorphoSource <https://www.morphosource.org/concern/media/000039626>). **C**, *Crocodylus johnstoni*, QMJ58446, skull in dorsal view. **D**, *Crocodylus porosus*, QMJ48127, skull in dorsal view.

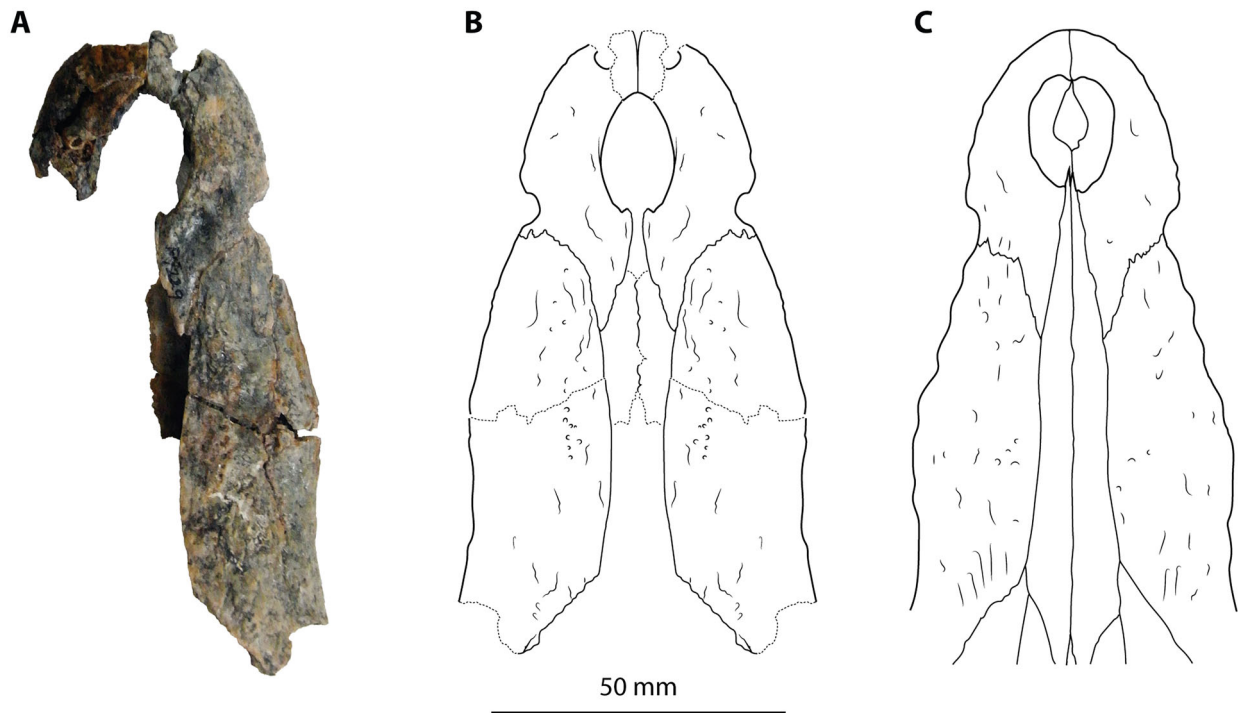


Figure 18. **A**, *Crocodylus* sp. QMF9229, partial rostrum from the Pliocene Allingham Formation, Bluff Downs Queensland. **B**, Reconstructed rostrum of QMF9229. **C**, Rostrum of equivalent-sized juvenile *Crocodylus porosus* (UQSSAL unregistered).

C. porosus of equivalent size (Fig. 18). Other Australian Pliocene fossils of *Crocodylus* potentially include isolated teeth with strong apicobasal fluting from Chinchilla on the Darling Downs, Queensland (Chiotakis 2018, 2019). Hocknull *et al.* (2020) suggested that the presence of strong fluting is diagnostic of *Crocodylus* within the context of the Late Cenozoic of Australia.

A novel species of *Crocodylus* has been reported, but not described, from the Pliocene–Pleistocene of the Lake Eyre Basin in the Tirari Desert of South Australia (Yates & Pledge 2017, Yates 2019). This species was included in a Bayesian tip-dated analysis (Lee & Yates 2018), which found it to belong to a clade of extralimital, non-crown group Pliocene–Pleistocene *Crocodylus*. If these results are correct,

then the Tirari Desert *Crocodylus* sp. and possibly all other Pliocene fossils of *Crocodylus* from Australia represent an early wave of immigration independent from the extant species.

Fragmentary cranial remains found at Tara Creek, a Pliocene locality in Queensland, were named *Crocodylus nathani* by Longman (1924). The systematic position of these remains has proved contentious, and they have been treated as a synonym of either *C. porosus* (Molnar, 1982b) or the mekosuchine *Paludirex gracilis* (as '*Pallimnarchus gracilis*': Willis & Molnar 1997a). The remains potentially include fossils of *Crocodylus* sp. but confirmation of this will require further study.

Molecular phylogenetic analyses indicate that the two extant Australian species of *Crocodylus*, *C. porosus* and *C. johnstoni*, are more closely related to extralimital species than to each other. In the case of *C. johnstoni*, its closest relatives are *Crocodylus novaeguineae* from New Guinea and *Crocodylus mindorensis* Schmidt, 1935 from the Philippines, whereas the closest relatives of *C. porosus* are the Asian *Crocodylus siamensis* Schneider, 1801 and *Crocodylus palustris* Lesson, 1831 (Meredith *et al.* 2011, Oaks 2011). This indicates that the two extant Australian species are the result of two further independent colonizations of Australia by *Crocodylus*. *Crocodylus johnstoni* likely split from *C. novaeguineae* and *C. mindorensis* sometime in the Middle to Late Miocene (~14–10 Ma), according to both a tip-dated Bayesian analysis and a molecular clock estimate (Oaks 2011, Lee & Yates 2018). However, the sole published fossil record of *C. johnstoni* is Late Pleistocene in age (Willis & Archer 1990).

Crocodylus porosus has long been reported from the geological record of Australia, but it is only recently that fossil material that can be considered reliably identified has been described. Jack & Etheridge (1892) reported the species from several localities in their list of fossils from the 'post Tertiary' of Queensland. The material they listed now resides in the NHMUK. None of the material they list is specifically referable to *C. porosus*, and some fossils can be confidently excluded from this species (JR and AMY pers. obs.). Molnar (1982b) referred several cranial fragments from the Pleistocene of the Darling Downs, Queensland, to *C. porosus*. However, none of these can be confidently referred to *C. porosus* on the basis of autapomorphies or a unique combination of derived characters. Indeed, one of these specimens, a premaxilla (QMF11626), is now referred to *Paludirex vincenti* (Ristevski *et al.*, 2020a), and others may yet be identified as belonging to other taxa (AMY pers. obs.). Hocknull *et al.* (2020) reported remains from the South Walker Creek area in north-eastern Queensland that they referred to *Crocodylus* sp. cf. *C. porosus*. The referral was based on derived osteoderm characteristics including thick, circular to ovoid bases, irregular, ragged edges, irregular pitting and tall, curved keels. The absence of an anterior external articular face can also be added to these characteristic features. These characteristics are unique to *C. porosus* when compared with mekosuchines, gavialoids and other species of

Crocodylus. The South Walker Creek specimens come from two sites dated to ~47.7 ka and ~40.1 ka. Interestingly, the oldest fossil bearing unit at South Walker Creek is dated to ~65.6 ka and lacks specimens referable to *Crocodylus* sp. cf. *C. porosus*, raising the possibility of an extremely late arrival of the species in Australia.

Gavialoidea

'*Gavialis papuensis*'

In 1905, Charles Walter de Vis reported fragmentary crocodylian remains recovered from Busai, Muyua (also known as Woodlark Island) in the Solomon Sea. After giving a description of the fossils, de Vis (1905) provisionally referred them to the genus *Gavialis* Oppel, 1811, under the specific name *G. papuensis*. Almost eight decades after the original study by de Vis (1905), the material was reviewed by Molnar (1982a), who concluded that referral to the genus *Gavialis* was invalid. The remains (Fig. 19) are considered to be likely derived from Quaternary sediments (Molnar 1982a, Lees 1986, Willis 1987, Markwick 1998, Mead *et al.* 2002, Riff *et al.* 2009), and consist of two osteoderms, six partial vertebrae, and three incomplete mandibular pieces. In addition to these elements, Molnar (1982a) also reported an isolated tooth crown that may be related to the same taxon (Fig. 19D). As the crocodylian remains were found alongside fossils of a marine turtle and a sirenian (de Vis 1905), Molnar (1982a) suggested a possible lagoonal or marine habitat for '*Gavialis papuensis*'. The incomplete mandibular pieces (Fig. 19A–C) are narrow and elongated, which is indicative of a slender longirostrine snout, and are further characterized by laterally oriented alveoli (de Vis 1905, Molnar 1982a). Molnar (1982a) compared the mandibles of the 'Muyua crocodylian' (= 'Murua crocodylian': Molnar 1982a; 'Murua crocodile': Willis 1987) with several slender longirostrine taxa and found them most comparable to *Charactosuchus* Langston 1965, *Ikanogavialis* Sill, 1970, and *Euthecodon* Fourtau, 1920, but a formal generic designation was not given due to the limited inferences permitted by the material at hand. Later, Aoki (1988) and Molnar (1993) considered the possibility that the remains of the 'Muyua crocodylian' may belong to a malformed individual of *Gavialis bengawanicus* Dubois, 1908, a gavialid from the Pleistocene of southeast Asia (Delfino & De Vos 2010, Martin 2019). Rauhe *et al.* (1999) suggested that the 'Muyua crocodylian' is referable to the genus *Ikanogavialis*, a gavialid known exclusively from the South American Neogene (Sill 1970, Salas-Gismondi *et al.* 2016). Several studies have regarded '*Gavialis papuensis*' as a gavialoid (Brochu 2001, 2003, 2006, Vélez-Juarbe *et al.* 2007, Jouve *et al.* 2008, Wheatley 2010). Delfino & De Vos (2010) considered '*Gavialis papuensis*' a *nomen dubium* due to the fragmentary nature of the specimens and their apparent lack of diagnostic features, but suggested that it likely represents an undetermined species of *Gavialis* (Delfino & De Vos 2010, p. 440). Martin *et al.* (2012) expressed uncertainty about the generic referral of the 'Muyua crocodylian', but stated that attribution to *Gavialis* is unlikely. Most recently, Rio & Mannion (2021)

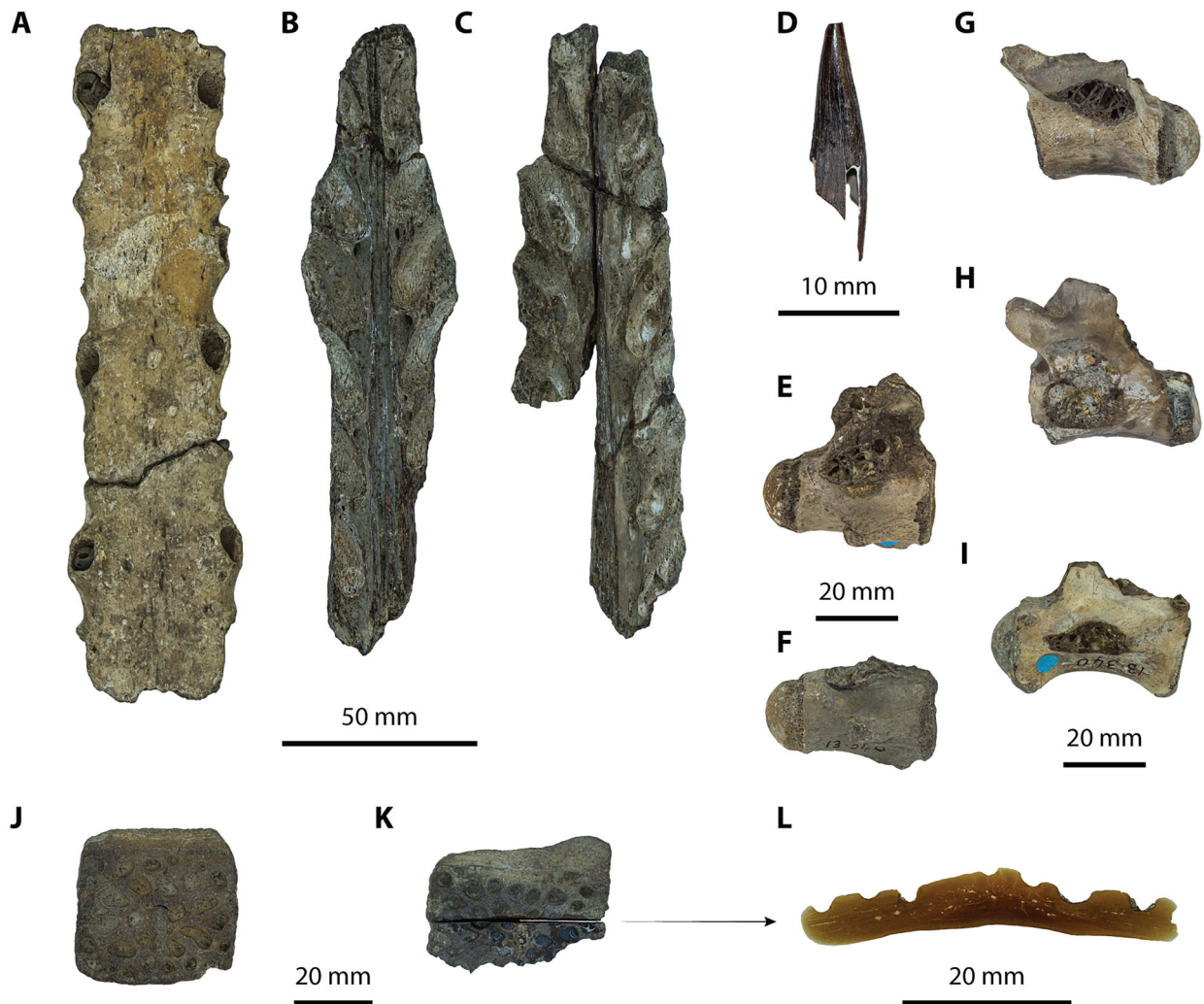


Figure 19. '*Gavialis papuensis*'. A, B, C, QMF406, mandibular fragments in dorsal views. D, Isolated tooth crown, unnumbered QMF specimen. E, F, QMF340, partial cervical vertebrae in right lateral views. G, QMF340, partial dorsal vertebra in left lateral view. H, QMF340, partial sacral vertebra (tentatively interpreted as a second sacral) in right lateral view. I, QMF340, partial caudal vertebra in right lateral view. J, QMF341, isolated osteoderm in dorsal view. K, QMF341, isolated osteoderm in dorsal view. Note that the osteoderm in K has a thin-section shown in L.

remarked that the material assigned to '*G. papuensis*' is not diagnostic at a species level, with these authors further noting that it may be attributable to the genus *Gavialis*. The phylogenetic affinities of the 'Muyua crocodylian' are still unresolved, and discovery of new and more complete remains from Muyua are needed to unravel this taxonomic mystery.

Gunggamarandu

The genus *Gunggamarandu* contains a single species, *Gu. maunala*, which is known from a partial cranium (Fig. 20). The holotype specimen of *Gu. maunala*, QMF548 (=QMF14.548, old registry number) was discovered on the Darling Downs, southeastern Queensland, some time in the nineteenth century (Ristevski *et al.* 2021). However, it is unclear if the holotype derives from Pliocene or Pleistocene sediments due to lack of information as to where exactly on the Darling Downs it was found (Ristevski *et al.* 2021). The first report on QMF548 was by Salisbury *et al.* (1995), who tentatively suggested gavialoid affinities for this species. Since the holotype and thus far only known specimen of

this taxon originates from the Darling Downs, it marks the southern-most known record of Gavialoidea from Australasia. *Gunggamarandu maunala* has a peculiar cranial morphology that is characterized by proportionally large supratemporal fenestrae, a deeply concave cranial table, and a supraoccipital with a convex occipital lamina and very large and widely spaced postoccipital processes (Ristevski *et al.* 2021, see also supplemental document S3 of Ristevski *et al.* 2023). Because of the incomplete preservational state of QMF548, an accurate TL estimate for the species is difficult, although the proportions of the specimen indicate that *Gu. maunala* was one of the largest, if not the largest crocodyliform yet found from Australia. Some of the phylogenetic analyses conducted by Ristevski *et al.* (2021) recovered a monophyletic Brevirostres, where morphological 'tomistomines' were found as a subclade of Crocodylidae instead of Gavialidae. In those analyses, *Gunggamarandu* was found to be a 'basal tomistomine' (see figure 4 in Ristevski *et al.* 2021). However, most other phylogenetic analyses that have incorporated *Gu. maunala* (the EW method analysis: see supplemental document S2 of Ristevski

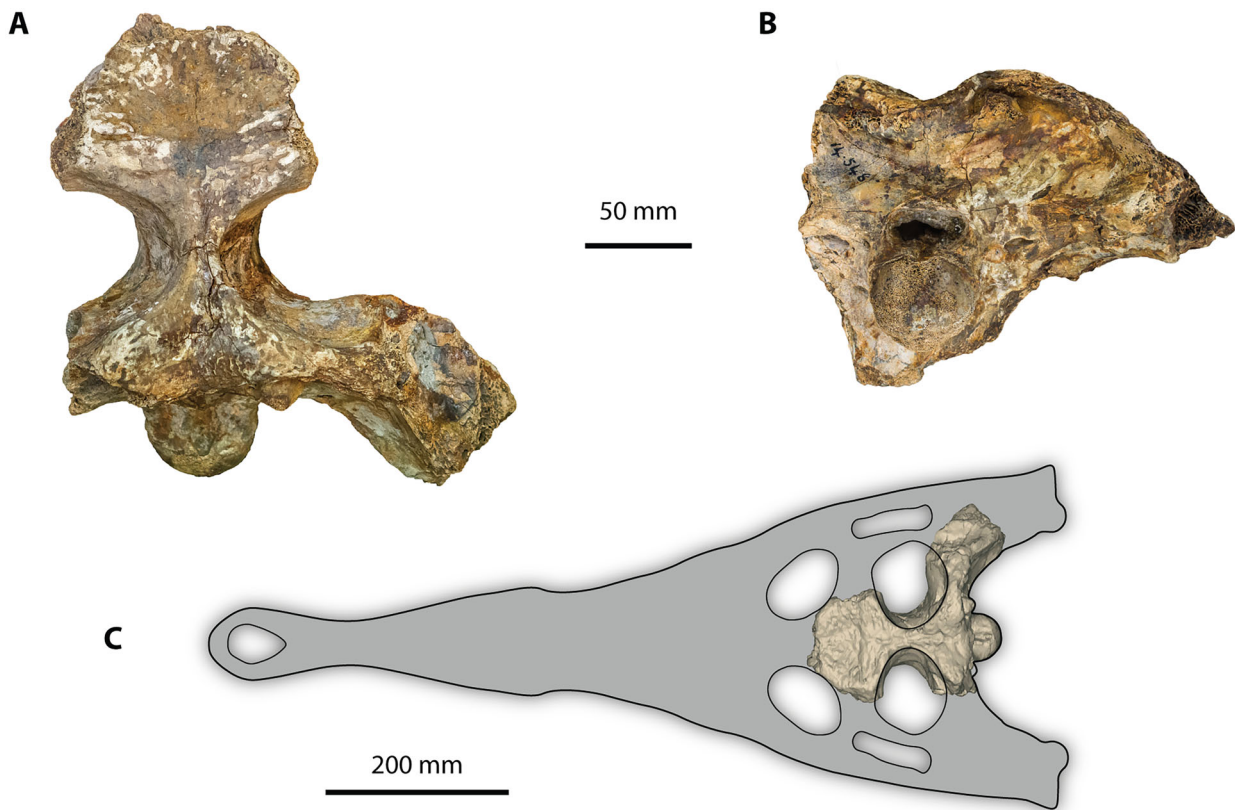


Figure 20. *Gunggamarandu maunala*. QMF548 (=QMF14.548, old registry number), holotype. **A**, Cranium in dorsal view. **B**, Cranium in posterior view. **C**, Hypothetical outline of the skull in dorsal view, with QMF548 depicted in its corresponding position (modified from Ristevski *et al.* 2021). Skull outline in C is based on skulls of *Dollosuchooides densmorei* and *Kentisuchus spenceri*.

et al. 2021, 2023) consistently recovered a monophyletic Longirostres and monophyletic Gavialoidea, where *Gu. maunala* was recovered as a non-gavialid gavialoid.

Harpacochampsia

The gavialoid genus *Harpacochampsia* also contains only one species, *H. camfieldensis*, known from the Middle Miocene Camfield Beds of the Bullock Creek LF, Northern Territory (Megirian *et al.* 1991). This taxon is represented by partially preserved craniomandibular elements and few isolated osteoderms (Fig. 21; Megirian *et al.* 1991). As inferred from the rostral fragment (NTM P87106-5; Fig. 21C), *H. camfieldensis* possessed a slender longirostrine snout with interlocking dentition (Megirian *et al.* 1991, see also supplemental document S3 of Ristevski *et al.* 2023). Willis (1997b) suggested that the inferred rostral morphology of *H. camfieldensis* is indicative of a mainly piscivorous diet, although Megirian *et al.* (1991) proposed that it may have also incorporated turtles and possibly even medium-sized mammals (see also Murray & Vickers-Rich 2004).

For decades, the phylogenetic placement of *Harpacochampsia* has been controversial and difficult to ascertain (Megirian *et al.* 1991, Brochu 2003). Some considered *H. camfieldensis* to be a mekosuchine (Willis 1995, 1997b; Brochu 2001, Jouve *et al.* 2008, 2015, Jouve 2016, Stein *et al.* 2016, Iijima & Kobayashi 2019, Stockdale & Benton 2021, Iijima *et al.* 2022), while others failed to recover it within Mekosuchinae or Gavialoidea (Salisbury &

Willis 1996, Molnar *et al.* 2002, Ristevski *et al.* 2020a, 2021). That *Harpacochampsia* is most likely a gavialoid was first proposed Yates & Pledge (2017), a hypothesis later supported by results from cladistic analyses by Lee & Yates (2018). More recent studies have agreed with the placement of *Harpacochampsia* within Gavialoidea (Rio & Mannion 2021, Ristevski *et al.* 2023), although it has been recovered as both a non-gavialid gavialoid and a gavialid gavialoid (Figs 24, 25; Ristevski *et al.* 2023). Discovery of more complete specimens will help with determining its precise position within Gavialoidea.

Other indeterminate crocodylians

'Eumeralla Formation taxon'

Crocodyliform remains of currently undetermined taxonomic affinities are known from the early Albian (Early Cretaceous; 113–108 Ma) Eumeralla Formation of Dinosaur Cove, Victoria (Willis 1997, 2006, Salisbury *et al.* 2003, Poropat *et al.* 2018, Paragnani *et al.* 2019, Wagstaff *et al.* 2020). This material represents the southern-most known record (as well as highest palaeolatitude, ~70°S) of Crocodylomorpha in Australia (Fig. 2; Paragnani *et al.* 2019). According to Paragnani *et al.* (2019), the Dinosaur Cove material is fragmentary and is represented by "... a quadratojugal, 28 teeth, a dorsal vertebra, a humerus and five osteoderms..." (see also Willis 2006, p. 332). A partial crocodylomorph osteoderm from the Eumeralla Formation

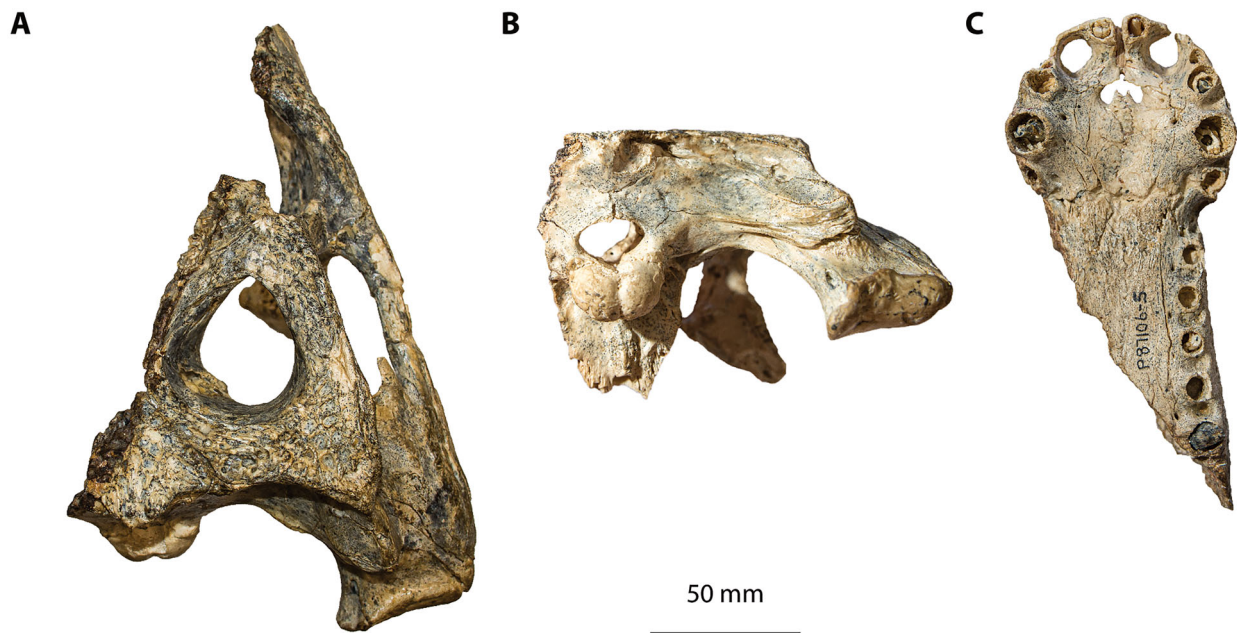


Figure 21. *Harpacochampsia camfieldensis*. **A**, Holotype cranium, NTM P87106-1, in dorsal view. **B**, Holotype cranium, NTM P87106-1, in posterior view. **C**, Partial snout, NTM P87106-5, in ventral view.

was figured by Poropat *et al.* (2018). Salisbury *et al.* (2003) suggested the material could be assigned to Susisuchidae. Paragnani *et al.* (2019) described the isolated teeth as non-ziphodont, but the fragmentary nature of the material prevents confident classification beyond Mesoeucrocodylia indet.

'Runcorn taxon'

An anterior portion of a right dentary, along with an associated tooth and a partial vertebral centrum, represent the oldest known crocodylian fossils from the Cenozoic of Australasia (Fig. 22; Willis & Molnar 1991a). These fossils were recovered from a well in Runcorn (a suburb of Brisbane), southeastern Queensland, and are most likely derived from the Paleogene Corinda Formation, with the fossils themselves thought to be early Eocene in age (Willis & Molnar 1991a). Initially, the 'Runcorn crocodylian' was considered as a possible longirostrine taxon (Willis & Molnar 1991a); however, Willis (1995) disagreed with this interpretation. Based on our observations of the dentary (Fig. 22A, B), it appears that its proportions are more akin to those of a mesorostrine crocodylian such as *C. porosus*. Thus, we also disagree with the slender longirostrine interpretation for the dentary fragment. Affinities of the 'Runcorn taxon' are uncertain, although it can be concluded that it is from a eusuchian crocodyliform due to the strongly procoelous centrum (Fig. 22C; Willis & Molnar 1991a). Because this material does not preserve autapomorphic features, its taxonomic relationships within Crocodylia remain inconclusive, although mekosuchine affinities have been tentatively proposed in the past (Willis & Molnar 1991a, Willis 1995, Buchanan 2009). Willis (1997b, 2006) suggested that the 'Runcorn taxon' may be referable to the genus *Kambara*;

however, the preservational condition of the material is insufficient to confidently support this referral.

'Geebung taxon'

In June 2013, a construction crew at Geebung (a suburb of Brisbane) recovered fragmentary fossil remains, including crocodylian, from a site that is considered to be Eocene in age. This material is undescribed and unpublished, and thus the taxonomic referral of the crocodylian fossils remains undetermined. It is possible that the material is of equivalent age to that from Runcorn, and could pertain to one small depositional basin that occurred in the Brisbane area during the Paleogene.

'Darling Downs taxon'

Ristevski *et al.* (2020a) reported two fragmentary specimens (QMF1151 and QMF1154) that represent a new taxon from the Darling Downs region. These specimens are partial premaxillae (and in the case of QMF1154, a fragment of a maxilla) that have a similar morphology to the premaxilla of *Paludirex vincenti*, such as subcircular alveoli, non-ziphodont teeth, an arching at the anterior of the alveolar processes, and overall comparable proportions. However, these premaxillae (Fig. 23A–D) differ from *P. vincenti* and *P. gracilis* in that: the 1st alveolus is positioned anteromedially to the 2nd; there is an insignificant interalveolar gap between the 1st and 2nd premaxillary alveolus; the 3rd and 4th premaxillary alveoli are of subequal size; and the posterior margin of the external narial fenestra is close to transverse. Specimen QMF1154 comes from the Pliocene Chinchilla LF on the Darling Downs. A premaxilla and maxilla fragment from the Pleistocene of the Clifton area on the Darling Downs, NHMUK PV OR 43047a (Fig. 23E, F),

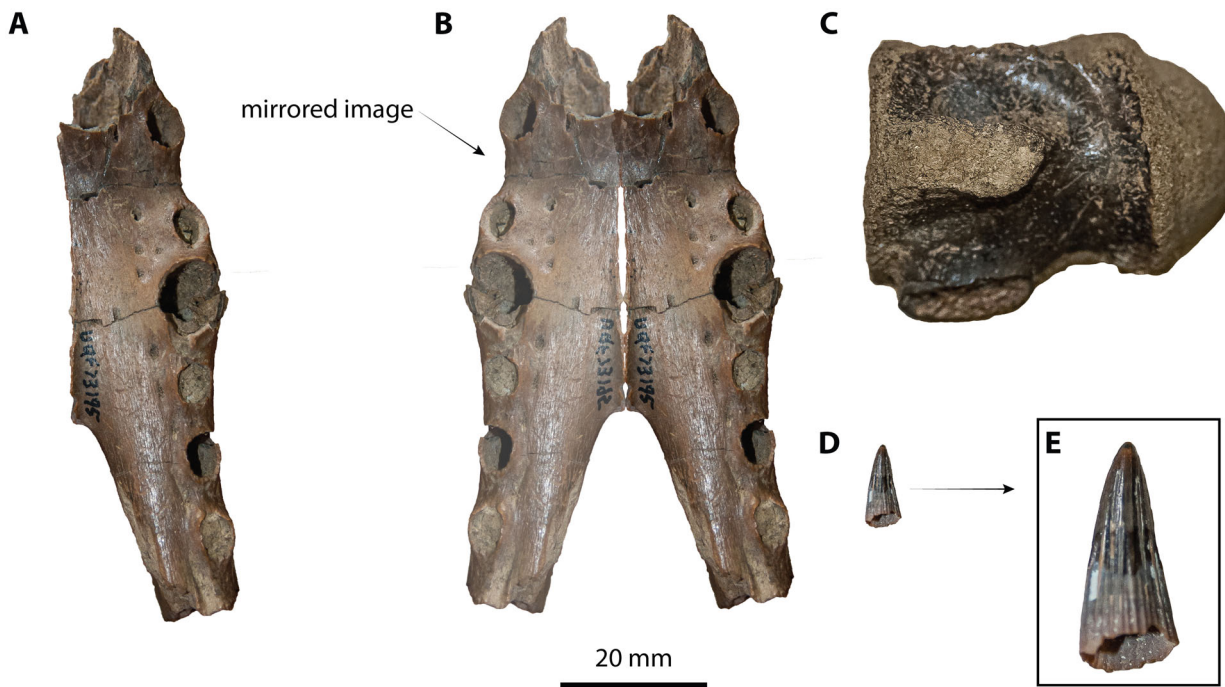


Figure 22. ‘Runcorn taxon’. A, QMF73195 (formerly UQF73195), anterior dentary piece in dorsal view. B, QMF73195, reconstructed anterior mandibular portion in dorsal view. C, QMF12363 (formerly UQF12363), cervical centrum in left lateral view. Isolated crocodylian tooth associated with QMF73195 in lingual view; D, scaled to the dentary fragment and centrum; E, scaled for visualization.

shares the same morphological features as QMF1151 and QMF1154. Lydekker (1888) was the first to mention NHMUK PV OR 43047a, but erroneously referred it to *C. porosus*. Considering the significant morphological differences, it can be concluded that the ‘Darling Downs taxon’ is neither *P. vincenti* nor *P. gracilis*. It is possible that it represents a third species of *Paludirex*, but it is equally likely that it belongs to a new genus. Their fragmentary nature prohibits reaching a conclusion on this matter, and therefore, like Ristevski *et al.* (2020a), we tentatively refer these specimens (QMF1151, QMF1154, and NHMUK PV OR 43047a) as *Paludirex?* sp. nov.

‘Bannockburn Formation taxon’

The presence of crocodylians in Aotearoa/New Zealand during the Cenozoic was first reported by Molnar & Pole (1997), who described a right angular. The angular (OU 22228) was recovered from the Early Miocene Bannockburn Formation near St. Bathans, Central Otago, South Island. The taxonomic affinity of this crocodylian is undetermined, although some authors have suggested that it may be a potential mekosuchine (Mead *et al.* 2002, Molnar *et al.* 2002, Holdaway & Worthy 2006, Willis 2006, Schwarzahns *et al.* 2012, Mather *et al.* 2019, Rio & Mannion 2021). Unfortunately, a conclusive classification is currently hampered by the fragmentary nature of OU 22228 and, therefore, this crocodylian remains unnamed and its possible mekosuchine affinities are yet to be tested. More recent reports of newly discovered crocodylian elements from the Bannockburn Formation hold promise for resolving the identification and taxonomic affinities of this crocodylian

(Pole *et al.* 2003, Worthy *et al.* 2006, 2009), including the possible presence of two taxa (see Salisbury *et al.* 2017).

Results of the phylogenetic analyses

As in Ristevski *et al.* (2023), the phylogenetic analyses performed here also resulted in generally consistent and largely resolved topologies (Figs 24–26, Table 3; Supplemental Data S2). The recovered cladograms had either entirely resolved (in four of the eight analyses) or almost completely resolved (in two of the eight analyses) relationships. Only one analysis (run under the NTS option and using the EW method) resulted with a poorly resolved topology. The nodal support tended to be relatively weak for most clades.

In all analyses, *Confractosuchus sauroktonos* was recovered as a sister taxon to Susisuchidae (*Isisfordia duncani* + *Susisuchus anatoceps*). Seven analyses recovered the *Co. sauroktonos* + Susisuchidae clade outside of Eusuchia (Fig. 24 and Supplemental Data S2), whereas one analysis found this clade as part of Eusuchia (Figs 25, 26). All other Australasian OTUs were recovered within Crocodylia.

Although the interrelationships of the major clades within Crocodylia were generally consistent in all analyses, the results from some analyses (e.g., Figs 25, 26) have intriguing implications for Mekosuchinae (read below). All eight analyses consistently recovered a monophyletic Longirostres (Crocodyloidea + Gavialoidea). As in Ristevski *et al.* (2023), *Gunggamarandu maunala* and *Harpacochampsa camfieldensis* were found within Gavialoidea. In all analyses, *Gu. maunala* was recovered as a non-gavialid gavialoid, and usually as a sister taxon to the European gavialoid *Dollosuchoides densmorei* Brochu, 2007b. *Harpacochampsa*

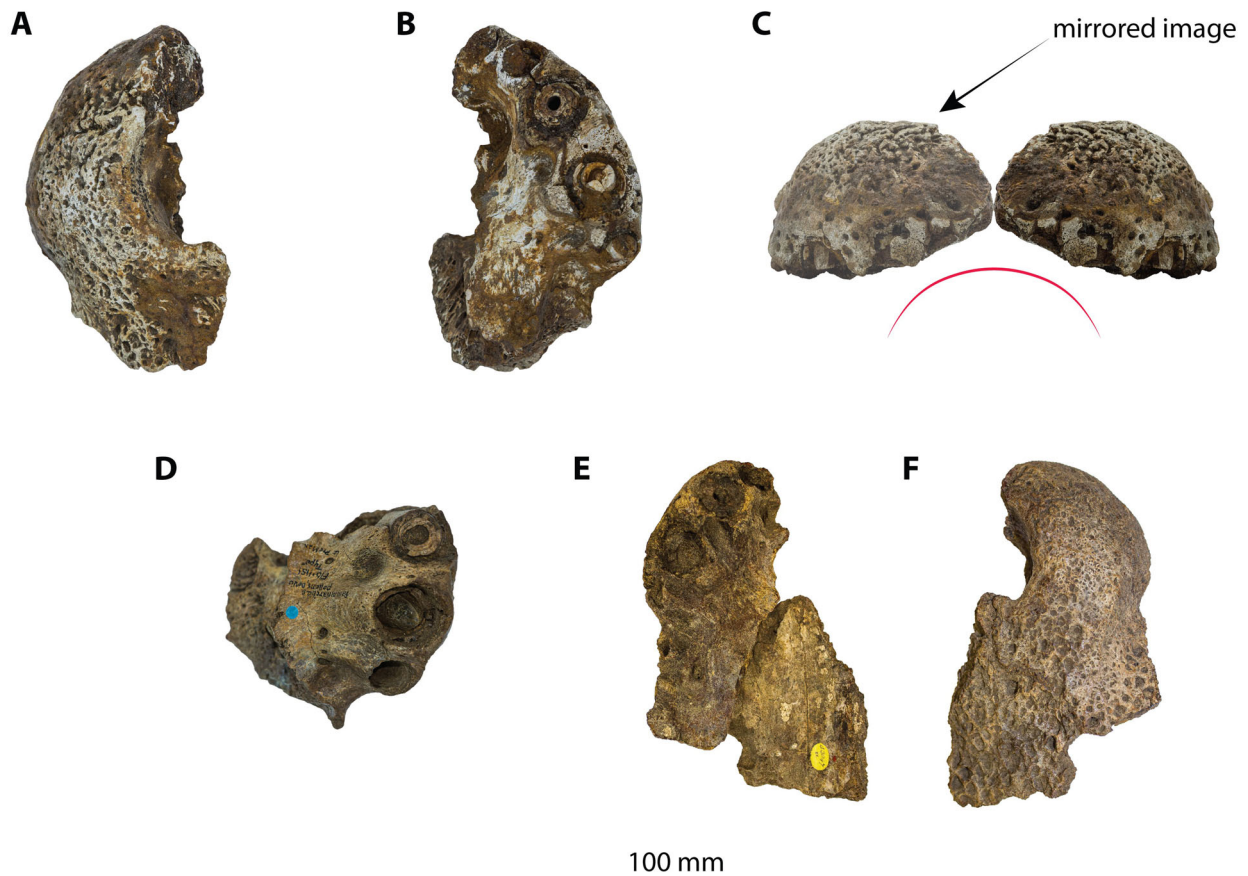


Figure 23. ‘Darling Downs taxon’ (= *Paludirex?* sp. nov.). QMF1154, left premaxilla and fragment of maxilla in A, dorsal and B, ventral views. C, QMF1154, premaxilla in anterior view, with the indicated mirrored photograph in order to aid comparison (modified from Ristevski *et al.* 2020a). the curved red line in C indicates the anterior arching of the premaxilla. D, QMF1151, incomplete left premaxilla in ventral view. NHMUK PV OR 43047a, right premaxilla and fragment of maxilla in E, ventral and F, dorsal views.

camfieldensis was recovered as a gavialid gavialoid in six out of eight analyses, whereas two analyses found *H. camfieldensis* as a non-gavialid gavialoid. None of the analyses recovered a sister-taxon relationship between *Gu. maunala* and *H. camfieldensis*.

Mekosuchinae was recovered as a monophyletic clade within Crocodyloidea in six out of the eight analyses (Fig. 24). The analyses that recovered a monophyletic Mekosuchinae found it as a sister clade to Crocodylidae. The basal-most mekosuchine differed between analyses, with *Australosuchus clarkae* recovered in that position in four analyses. *Kalthifrons aurivellensis* was found as the basal-most mekosuchine in one topology (Fig. 24), whereas *K. aurivellensis* + *Kambara* spp. was recovered as the basal-most mekosuchine clade in one of the analyses. All other mekosuchines comprised a monophyletic Mekosuchini. There were two recovered subclades within Mekosuchini: one subclade comprising the small-bodied and/or insular taxa (*Baru huberi* + *Trilophosuchus rackhami* + *Volia athollandersoni* + *Mekosuchus inexpectatus*; the insular taxa are *M. inexpectatus* and *V. athollandersoni*), and a second subclade comprising large-bodied taxa from continental Australia (*Baru* + *Paludirex* + *Quinkana*). The subclade formed by the small-bodied taxa had *B. huberi* recovered in a basal position to the clade comprising *T. rackhami* + (*V. athollandersoni* + *Mekosuchus*). The subclade comprised of

the large-bodied Australian taxa usually found *Paludirex* as the sister taxon to the *Baru* + *Quinkana* clade, except in one analysis where *Paludirex* was the sister taxon to *Baru* (Figs 25, 26).

Arguably, the most intriguing results from the phylogenetic analyses concern the alternative composition and placement of Mekosuchinae. Two of the eight analyses resulted with a paraphyletic Mekosuchinae that incorporates Orientalosuchina (Figs 25, 26; Supplemental Data S2), a group of Cretaceous–Paleogene crocodylians from Asia that has been regarded as a subclade of Alligatoroidea (Massonne *et al.* 2019, Shan *et al.* 2021; in six of our analyses, Orientalosuchina was also recovered within Alligatoroidea). The first of these two analyses (run under the TrS option and using the EW method; Figs 25, 26) recovered *A. clarkae* and *Kambara* spp. outside of Mekosuchinae. In this analysis, *A. clarkae* was found as the basal-most crocodyloid, whereas *Kambara* spp. was the sister group to Crocodylidae. All other mekosuchines fell outside of Longirostres and formed a monophyletic clade that also included orientalosuchins. In the strict consensus results (Fig. 25), Mekosuchinae was part of a larger polytomy within Eusuchia. The 50% majority-rule consensus (Fig. 26) depicts a better resolved topology, where *Asiatosuchus germanicus* Berg, 1966 was the sister taxon to Mekosuchinae. In this analysis, Mekosuchinae was

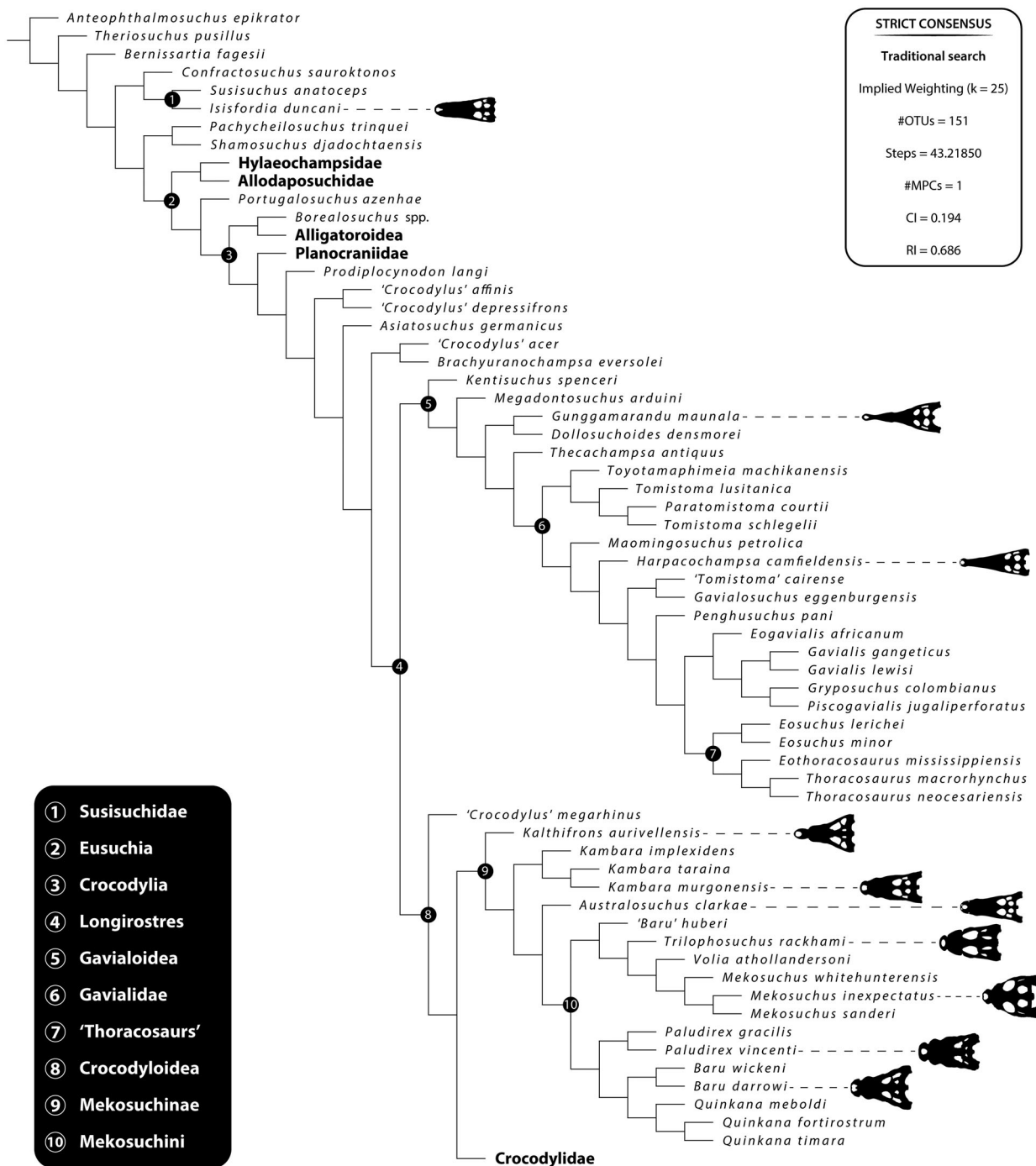


Figure 24. Strict consensus of a single fully resolved most parsimonious cladogram from the analysis run under TrS, and a weighting strength of $k = 25$. See Supplemental Data S2 for additional information. Abbreviations: CI, consistency index; #MPCs, number of most parsimonious cladograms; #OTUs, number of operational taxonomic units; RI, retention index.

comprised of two major subclades: one subclade including continental Australian taxa (*Kalthifrons* + (*Quinkana* + (*Baru* + *Paludirex*))), and a second subclade that includes Orientalosuchina and the small-bodied and/or insular taxa (*B.* *huberi* + *T. rackhami* + *V. athollandersoni* + *Mekosuchus*). Massonne *et al.* (2019) also assigned the Asian taxon *Protoalligator huiningensis* Young, 1982 to Orientalosuchina; however, in this analysis this taxon was recovered outside of that clade (Fig. 25). Within Mekosuchinae, Orientalosuchina formed a separate

monophyletic subclade, except for *Dongnanosuchus hsui* Shan *et al.*, 2021, which did not cluster with the other orientalosuchins, but instead was found to be the sister taxon to the (*B.* *huberi* + *T. rackhami* + *V. athollandersoni* + *Mekosuchus*) clade.

The second analysis that resulted in a paraphyletic Mekosuchinae was run under the NTS option and used the EW method. However, out of the eight performed analyses, this one resulted in the most poorly resolved strict consensus topology. The 50% majority-rule consensus of this

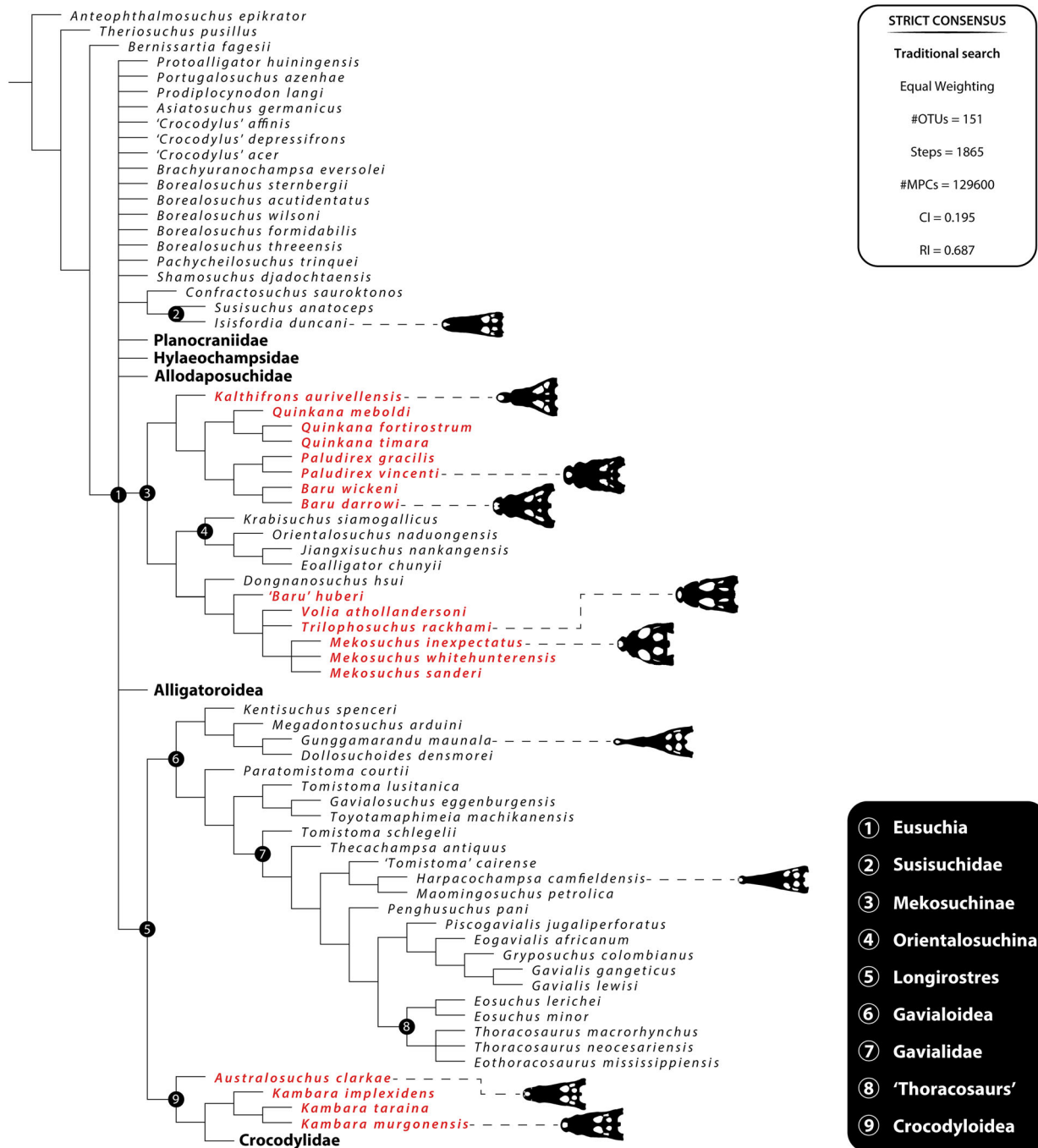


Figure 25. Strict consensus of 129600 MPCs from the analysis run under TrS, without IW. The results from this analysis point towards an alternative position for Mekosuchinae than that recovered in other analyses. Australasian mekosuchines are highlighted in red. See [Supplemental Data S2](#) for additional information. Abbreviations: CI, consistency index; #MPCs, number of most parsimonious cladograms; #OTUs, number of operational taxonomic units; RI, retention index.

analysis depicted a relatively resolved cladogram, where Mekosuchinae also included Orientalosuchina and formed a subclade of Crocodylidae (see [Supplemental Data S2](#)).

Comparisons between Australasian mekosuchines and Asian orientalosuchins

The results from the TrS EW analysis indicated five synapomorphies for Mekosuchinae inclusive of Orientalosuchina: a splenial without an anterior perforation for the mandibular ramus of cranial nerve V (character 52, state 1); an angular

that does not extend dorsally beyond the anterior end of the foramen intermandibularis caudalis (character 65, state 1); a secondary choana that projects anteroventrally at maturity (character 122, state 1); the postorbital neither contacts the quadrate nor quadratojugal medially (character 143, state 0); and the minimum width between the supratemporal fenestrae with respect to the maximum cranial table width is at least 20% (character 206, state 2). The first of these synapomorphies (character 52, state 1) is ambiguous, as it occurs in many crocodylians and is not exclusive to mekosuchines or orientalosuchins. The second synapomorphy (character

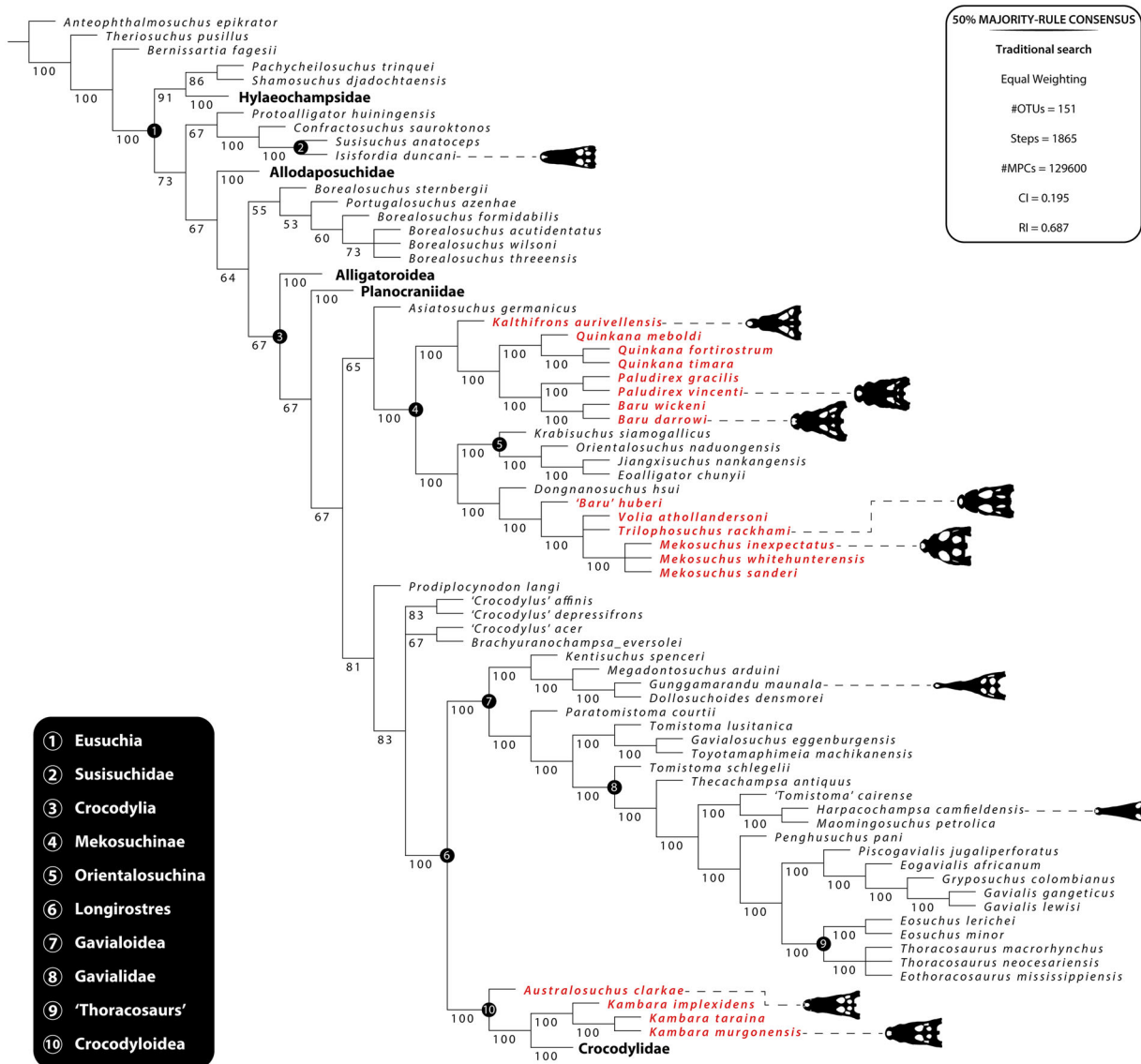


Figure 26. 50% majority-rule consensus topology from the analysis run under TrS, without IW. Australasian mekosuchines are highlighted in red. See Fig. 25 for the strict consensus topology of the same analysis. See Supplemental Data S2 for additional information. Abbreviations: CI, consistency index; #MPCs, number of most parsimonious cladograms; #OTUs, number of operational taxonomic units; RI, retention index.

Table 3. Summary of the phylogenetic results.

Search option	Weighting	k value (if IW)	Steps	#MPCs	CI	RI
Traditional	EW	–	1865	129600	0.195	0.687
Traditional	IW	5	112.54302	1	0.191	0.679
Traditional	IW	12	71.07717	2	0.193	0.683
Traditional	IW	25	43.21850	1	0.194	0.686
New Technology	EW	–	1864	182	0.195	0.688
New Technology	IW	5	112.54248	1	0.191	0.679
New Technology	IW	12	71.07490	2	0.193	0.683
New Technology	IW	25	43.19272	1	0.195	0.686

Abbreviations: CI, consistency index; EW, equal weighting; IW, implied weighting; #MPCs, number of most parsimonious cladograms; RI, retention index.

65, state 1) is similarly inconclusive, since it is unknown for most mekosuchines and it also occurs in many alligatoroids. The third synapomorphy (character 122, state 1) is unknown for most Australian mekosuchines, although it is present in species of *Baru*, whereas *Kambara implexidens* and *Kambara taraina* differ in this regard by possessing a posteroventrally projecting secondary choana (character 122, state 0).

An anteroventrally projecting secondary choana is present in all orientalosuchins that could be scored for this character. Outside of Mekosuchinae and Orientalosuchina, an anteroventrally oriented secondary choana is common in Alligatoroidea. The fourth synapomorphy (character 143, state 0) occurs in *Australosuchus clarkae*, *K. implexidens*, *Paludirex vincenti*, *Quinkana timara*, as well as *Krabisuchus siamogallicus* Martin & Lauprasert, 2010 and *Jiangxisuchus nankangensis* Li et al., 2019; it is unknown in other mekosuchines and orientalosuchins. However, this is another feature that is common in many crocodylians, and is not unique to these mekosuchines and orientalosuchins. The final synapomorphy (character 206, state 2) occurs in some mekosuchines and orientalosuchins (unknown for *Baru darrowi*, *Mekosuchus whitehunterensis*, *Paludirex gracilis* and *Quinkana fortirostrum*). However, *A. clarkae*, *M. inexpectatus*, *J. nankangensis* and *Orientalosuchus naduongensis* Massonne et al., 2019 differ from the other taxa in the scoring

of this character (character 206, state 1). Yet again, state 2 of character 206 is a feature that is not exclusive to mekosuchines and orientalosuchins as it occurs in other crocodylians, most often alligatoroids. Thus, the indicated synapomorphies from the analysis do not unambiguously support Orientalosuchina as a subclade of Mekosuchinae.

There are additional morphological similarities between some orientalosuchins and mekosuchines that were not specified in the synapomorphy list from the analysis. One of the most notable features is the presence of ridges on the pterygoid plates situated laterally to the secondary choana (character 215, state 1). These pterygoid ridges were first reported by Salisbury & Willis (1996) for *Kambara* spp., and later by Buchanan (2009). These types of ridges were also recognized by Yates (2017) and Yates & Pledge (2017) in *Kalthifrons aurivellensis* and *Baru* spp. (see also Rio & Mannion 2021). *Dongnanosuchus hsui* also appears to possess such ridges (see figures 3.3, 3.4 and 5.5 in Shan *et al.* 2021). Therefore, these pterygoid ridges are, at present, known exclusively for some mekosuchines and *D. hsui*.

In addition to the anteroventrally projecting secondary choana (character 122, state 1), some mekosuchines and orientalosuchins share a choana with an invaginated anterior margin (character 250, state 1; occurs in *Baru wickeni*, *M. inexpectatus*, *D. hsui* and *K. siamogallicus*); however, some mekosuchines have a straight anterior margin of the choana, such as *Trilophosuchus rackhami*. An invaginated anterior margin of the secondary choana is also present in many alligatoroids.

In some Mekosuchini, the suborbital fenestrae extend far anteriorly relative to the maxillary alveoli, up to the level of the seventh or even sixth alveoli (character 201, state 2; e.g., *Baru* spp., *Mekosuchus* spp., *Q. babarra*, *Q. fortirostrum*, *T. rackhami*; see also supplemental document S1 of Ristevski *et al.* 2023). This feature is exclusive to the members of Crocodylia that were included in our phylogenetic dataset. Other mekosuchines and many crocodylians have suborbital fenestrae that extend anteriorly up to the level of the eighth maxillary alveoli (character 201, state 1), such as *D. hsui* or *O. naduongensis*. However, most crocodylians have suborbital fenestrae that terminate at the level of the ninth alveoli or even posterior to them (character 201, state 0). Additionally, some but not all mekosuchines have relatively short anterior processes of the palatines (character 115, state 1; e.g., *Baru* spp., *Ka. taraina* and *Q. fortirostrum*). Orientalosuchins also have short anterior palatine processes (*D. hsui*, *Or. naduongensis* and *J. nankangensis*), although this feature is not exclusive to mekosuchines nor orientalosuchins as it is present in other crocodylians (e.g., some osteolaemines and some stem Longirostres). Thus, even though the orientalosuchin suborbital fenestrae do not extend as far anteriorly as in some Mekosuchini, and the short anterior process of the palatines is present in many crocodylians, it is notable that the orientalosuchins do share these features with some mekosuchines to a certain degree.

In some, but not all mekosuchines, the pterygoid has a well-developed anterior process that forms a significant (more than 20%) portion of the interpalatal bar (the rest is

formed by the palatines; character 118, state 2). This is the condition in '*B. huberi*', *M. inexpectatus* and *T. rackhami* (e.g., figures 2B and 13D in Ristevski *et al.* 2023). The same condition is also present in *D. hsui* and *O. naduongensis*.

A meatal chamber with a posterior margin that is smooth and continuous with the paroccipital process (character 148, state 1) occurs in all mekosuchines, where the squamosal is sufficiently preserved (*A. clarkae*, '*B. huberi*', *K. aurivellensis*, *Kambara* spp., *Mekosuchus sanderi*, *Q. timara* and *T. rackhami*). The same condition is present in *D. hsui*, *J. nankangensis*, *Or. naduongensis* and *Kr. siamogallicus*. Outside of Mekosuchinae, this state occurs in many gavialoids (including *H. camfieldensis*), some alligatoroids, *Prodiplacynodon langi* Mook, 1941, *Boverisuchus vorax* (Troxell, 1925), and *Borealosuchus formidabilis* (Erickson, 1976).

A supraoccipital with a prominent dorsal exposure on the cranial table (character 159, state 2) is present in several mekosuchines (e.g., *Baru* spp., *M. inexpectatus*, *T. rackhami*). Some mekosuchines have an evident dorsal exposure of the supraoccipital, although to a lesser degree (character 159, state 1; e.g., *K. aurivellensis*, *Kambara* spp., *V. athollandersoni*). The most extreme version of this condition within Mekosuchinae is recognized for *M. sanderi*, where the dorsal exposure of the supraoccipital excludes the parietal from participating in the posterior margins of the cranial table (character 159, state 3). A dorsal exposure of the supraoccipital on the cranial table was listed as one of the diagnostic traits for Mekosuchinae by Willis *et al.* (1993). However, a dorsal exposure of the supraoccipital is relatively common among Crocodylia and is far from unique to mekosuchines. Nevertheless, this feature is also manifested in varying forms among orientalosuchins. For example, *D. hsui* and *Kr. siamogallicus* are scored as state 2 for character 159 (like '*B. huberi*', *B. wickeni*, *M. inexpectatus* and *T. rackhami*), *J. nankangensis* as state 1 (like *K. aurivellensis*, *Kambara* spp., *V. athollandersoni*), and *O. naduongensis* as state 3 (like *M. sanderi*). Aside from '*B. huberi*', *B. wickeni*, *M. inexpectatus*, *T. rackhami*, *D. hsui* and *Kr. siamogallicus*, a large dorsal exposure of the supraoccipital that does not exclude the parietal from reaching the posterior edge of the cranial table (character 159, state 2) is present in some alligatoroids. Other than *M. sanderi* and *Or. naduongensis*, a large supraoccipital dorsal exposure that excludes the parietal from the cranial table edge is also present in some alligatoroids. Moreover, the dorsal exposure of the supraoccipital on the cranial table has a trapezoid outline in '*B. huberi*', *B. wickeni*, *T. rackhami*, *D. hsui*, *O. naduongensis* and *Kr. siamogallicus*, but also few alligatoroids (character 198, state 0).

The anterior alveolar processes of the premaxillae are inclined dorsomedially in some mekosuchines, such as *Paludirex* spp., resulting in an arch-like appearance of the snout when observed in anterior view (character 223, state 1; see Ristevski *et al.* 2020a). Similar 'arching' of the premaxillae also occurs in *D. hsui* (figures 3.1 and 3.2 in Shan *et al.* 2021) and *Or. naduongensis* (JR pers. obs. of GPIT/RE/09730; note that the premaxillae of GPIT/RE/09730 are incomplete anteriorly, although their preserved margins are indicative of similar 'arching' to that

in *D. hsui*). Other than some mekosuchines and the aforementioned orientalosuchins, anterior ‘arching’ of the premaxillae occasionally occurs (is polymorphic) in some alligatoroids (e.g., *Alligator* spp., *Caiman latirostris* [Daudin, 1802], *Paleosuchus* spp.).

A notable size disparity between the largest and smallest maxillary alveoli is another feature that Willis *et al.* (1993) listed in their original diagnosis for Mekosuchinae. This is evident in *A. clarkae*, *Baru* spp., ‘*B.* *huberi*, *M. inexpectatus*, *M. sanderi*, *P. vincenti*, but also *D. hsui* and *J. nankangensis*, where the diameter of the largest maxillary alveolus is at least twice that of the smallest interfestoonal alveolus (character 220, state 1). This feature also occurs in ‘*Crocodylus*’ *megarhinus* Andrews, 1905, a few alligatoroids, a few hylaeochampsids, some species of *Borealosuchus*, and the outgroup taxon in our analyses, *Anteophthalmosuchus epikrator*.

Another feature present only in some mekosuchines and orientalosuchins among the crocodylian taxa included in our analyses is the steep dorsal inclination of the posterior mandibular ramus (character 252, state 1). This is present in *Mekosuchus* spp. (*M. inexpectatus* and *M. whitehunterensis*; see Figs 12E, 13A) and *Or. naduongensis* (see Massonne *et al.* 2019).

Further regarding the mandible, *Or. naduongensis* also shares with species of *Mekosuchus* a retroarticular process that is on a ventral level relative to the articular fossa (character 254, state 0), and a similarly small and sub-elliptical external mandibular fenestra. Moreover, the angular and surangular of *Or. naduongensis* possess acute laterally projecting ridges. Admittedly, these mandibular features are not unique to *Or. naduongensis* nor species of *Mekosuchus*, and occur in some other mekosuchines but also other crocodylians and even non-crocodylian crocodyliforms.

Baru spp., *Mekosuchus* spp., *Or. naduongensis* and *Kr. siamogallicus* have a dentary with deep curvature between the fourth and tenth alveoli when observed in lateral aspect (character 50, state 1). Such deep curvature on the dentary is also present in certain alligatoroids (Brochu 1999). Lastly, the surangular–dentary suture intersects the external mandibular fenestra at its posterodorsal corner (character 64, state 1) in *M. inexpectatus*, *M. whitehunterensis*, *J. nankangensis*, *Or. naduongensis*, *Kr. siamogallicus*, but also some alligatoroids.

Although Australasian mekosuchines and Asian orientalosuchins share several morphological features, almost all of them also occur in other crocodylians, often alligatoroids. A feature that is shared exclusively between some mekosuchines and *D. hsui* are the pterygoid ridges. At present, the support for a close relationship between the Australasian mekosuchines and the Asian orientalosuchins is relatively weak, both from phylogenetic assessments and morphological observations of available specimens. It must be declared that all our observations on orientalosuchins were limited to the currently published literature and a handful of photographs from few specimens. Thus, it is certainly possible that there may be more shared features we were unable to observe from the sources available to us. Future studies should further explore whether there are additional

similarities between these Australasian and Asian crocodylians that support close relationships between these taxa, or if these are merely convergently acquired features.

Discussion

Australasian Mesozoic record of Crocodylomorpha

Material of Mesozoic crocodylomorphs from Australasia remains limited to the Early–Late Cretaceous of continental Australia (early Albian–early Turonian; Fig. 3). The oldest reported material (the ‘Eumeralla taxon’) is currently of undetermined taxonomic classification beyond Mesoeucrocodylia indet. Otherwise, the only named genera (*Confractosuchus* and *Isisfordia*) are either derived non-eusuchian neosuchians or basal eusuchians, although a consensus on this matter is yet to be reached. Thus far, the only published studies that incorporated *Confractosuchus sauroktonos* in phylogenetic analyses (White *et al.* 2022) resulted in different but not too dissimilar phylogenetic hypotheses. White *et al.* (2022) found *Co. sauroktonos* to be a basal eusuchian and a sister taxon to Suisuchidae + Hylaeochampsidae, whereas our analyses consistently recovered *Co. sauroktonos* as a sister taxon to Suisuchidae, and either as a non-eusuchian or a basal eusuchian.

Regardless of whether *C. sauroktonos* and the susisuchid *Isisfordia* spp. are derived non-eusuchian neosuchians or basal eusuchians, the Mesozoic record in Australia (and by extent, Australasia) is still represented by a relatively low taxonomic diversity of Crocodylomorpha when compared to other major Gondwanan landmasses except Antarctica (i.e., South America, Africa, Madagascar, and even the Indian subcontinent; e.g., Prasad *et al.* 2013). This is almost certainly due to the lack of known fossil material rather than genuinely low taxonomic diversity. As noted by Hart *et al.* (2021), the crocodylomorph faunas from Gondwana are characterized by a great diversity of notosuchian crocodyliforms, a clade that is absent from Australia. Plane (1967), Hecht & Archer (1977) and Archer (1978) reported fragmentary material from the Neogene of New Guinea and Neogene and Quaternary of continental Australia that were tentatively referred to the notosuchian subclade Sebecosuchia. However, there is no compelling support for the referral of this material to Sebecosuchia, and it is far more likely that these fossils represent mekosuchines instead (Molnar 1982c, Willis 1997b, Molnar *et al.* 2002, Wroe 2002, Brochu 2003). It is currently unclear if the absence of Notosuchia from Australasia’s fossil record is genuine and a probable consequence of a high-palaeolatitude barrier (Nicholl *et al.* 2021). Alternatively, the lack of notosuchian fossils from Australasia may simply be a result of sampling bias, and it is quite possible that notosuchian remains (or even remains of other non-neosuchian crocodylomorphs) will be discovered in the future.

The presence of susisuchids in Australia (*Isisfordia* spp.) and South America (*Suisuchus* spp.) is evidence of crocodyliform interchange between these two landmasses (Salisbury *et al.* 2003). Other groups of reptiles that are recognized from the fossil record of both South America and

Australasia include megaraptoran theropod dinosaurs and meiolaniform turtles, thus further supporting the reptilian faunal interchange between western and eastern Gondwana during the Cretaceous and/or early Paleogene (e.g., Megirian 1992, Gaffney *et al.* 1998, Smith *et al.* 2008, Agnolín *et al.* 2010, Sterli & de La Fuente 2011, Novas *et al.* 2013, de La Fuente *et al.* 2014, Sterli *et al.* 2015, Joyce 2017, Poropat *et al.* 2018). Madtsoiid snakes are yet another group of reptiles with a known fossil record from across Gondwana (except Antarctica), including Australia (e.g., Scanlon 2006b, Laduke *et al.* 2010). Considering the high taxonomic diversity of Notosuchia during the Late Cretaceous of South America (Pol & Leardi 2015), it would not be surprising if notosuchians also managed to reach Australia during this time. Future field work on Mesozoic fossil deposits from Australasia in general, and Australia in particular, can test this hypothesis.

Mekosuchinae

For much of the past three decades, the general consensus has been that Mekosuchinae is a crocodylid subclade (e.g., Willis *et al.* 1993, Brochu 2003). However, some phylogenetic analyses have recovered Mekosuchinae in a position outside of Crocodylidae (Salisbury & Willis 1996, Lee & Yates 2018, Cossette *et al.* 2020, Azzarà *et al.* 2021, Rio & Mannion 2021, Brochu *et al.* 2022, Ristevski *et al.* 2023). The phylogenetic results from this study corroborate the latter position, with Mekosuchinae recovered as either a sister clade to Crocodylidae (Fig. 24) or outside of Longirostres (Figs 25, 26). Whether Mekosuchinae is a basal clade of Crocodyloidea or a non-crocodyloid crocodylian clade is unclear, although most results from our study tend to favour the former hypothesis (also Ristevski *et al.* 2023). Ascertaining a more concrete phylogenetic position of the clade depends on scoring more morphological characters for the mekosuchine OTUs, as well as the discovery of more complete specimens of relevant taxa.

Is *Orientalosuchina* a subclade of *Mekosuchinae*?

One of the most intriguing results from our study is the phylogenetic placement of *Orientalosuchina* within Mekosuchinae (Figs 25, 26). Originally, Massonne *et al.* (2019) established the clade *Orientalosuchina* for several Late Cretaceous–Paleogene taxa from Asia, and regarded it as a subclade of Alligatoroidea (see also Shan *et al.* 2021). In our phylogenetic analysis, the nodal support for a paraphyletic Mekosuchinae (that excludes *Australosuchus* and *Kambara*) outside of Longirostres and incorporating *Orientalosuchina* was relatively weak. Furthermore, only two of the eight phylogenetic analyses performed herein recovered a relationship between *Orientalosuchina* and Mekosuchinae. Nonetheless, recovering the alternative phylogenetic placement and composition of *Orientalosuchina* and Mekosuchinae in some of our analyses deserves commenting.

In the results from one of the phylogenetic analyses, the crocodylian *Asiatosuchus germanicus* from the Eocene of Europe was found as the sister taxon to Mekosuchinae (Fig. 26). Previously, Salisbury & Willis (1996) also recovered *As. germanicus* as a sister taxon to Mekosuchinae, and recently Rio & Mannion (2021) found the enigmatic Asian crocodylian *As. nanlingensis* Young, 1964 deeply nested within Mekosuchinae. Thus, our results are not the first time a relationship between a species of *Asiatosuchus* Mook, 1940 and Mekosuchinae was recovered. Although nodal support for the placement of *As. nanlingensis* within Mekosuchinae was relatively weak in the analyses by Rio & Mannion (2021), it nevertheless marked the first study where an Asian taxon was recovered deeply nested within Mekosuchinae. Based on their results, Rio & Mannion (2021) proposed possible Asian origins for mekosuchines, a proposition that was also made by Scanlon (2014). According to some of our phylogenetic results, we also infer Asian origins for mekosuchines. Additionally, some of our results that found Mekosuchinae outside of Longirostres are not the first instances of this phylogenetic hypothesis, as some of the analyses by Lee & Yates (2018) also resulted with a stem Longirostres placement for Mekosuchinae.

Our study, and the one by Ristevski (2022c), are the only instances where *Orientalosuchina* was recovered as deeply nested within Mekosuchinae. At present, the phylogenetic placement of *Orientalosuchina* as a mekosuchine subclade is tentative, due to the relatively poor nodal support and the inconsistent recovery of this relationship. Nevertheless, there are certain morphological similarities between Australian mekosuchines and the *orientalosuchins* from Asia that support the possibility of close phylogenetic relationships. Perhaps the biggest obstacle in obtaining a more definitive answer on this matter is the fragmentary nature of some mekosuchines and *orientalosuchin* fossils that prevents more thorough morphological comparisons and scoring of phylogenetic characters. Hopefully, better-preserved fossils will come to light in the future that will clarify this relationship. In sum, we tentatively consider the taxa assigned to *Orientalosuchina* as probable mekosuchines due to some shared morphological similarities between these Asian and Australasian crocodylians, and the support for this relationship in some phylogenetic analyses. Doubtless, this is an important but unresolved question on crocodylian evolution and palaeobiogeography that is worthy of investigation by future studies.

On the possible origins of mekosuchines

If Mekosuchinae are outside of Longirostres and if *Orientalosuchina* is a subclade of Mekosuchinae, then this has major implications for the origins and diversity of mekosuchines. As stated above, these results would suggest that members of Mekosuchinae most likely originated in Asia during the Cretaceous, and they arrived in Australia from southeast Asia no later than the late Paleocene. Of note is the geographic distance between Australia and southeast Asia during the Late Cretaceous and early Paleogene, which was significantly greater than it is today.

If mekosuchines arrived in Australia from Asia during the Late Cretaceous–early Paleogene, then their dispersal would have involved a substantial marine trek and/or certain degree of ‘island hopping’ (assuming that some islands existed between Asia and Australia during the Late Cretaceous–early Paleogene). This scenario may also imply some form of osmoregulation in the ancestral mekosuchines. Extant crocodylids and gavialids possess salt-excreting glands on the keratinized buccal surfaces of their tongues, thus allowing them to traverse in saltwater (Taplin *et al.* 1982, 1985, Taplin 1988, Brochu 2003). Extant alligatorids, however, do not possess salt-excreting glands and therefore they do not frequent saltwater environments (Taplin *et al.* 1982, Leslie & Taplin 2001, Brochu 2003, Grigg & Kirshner 2015), although some extant alligatorids have been documented inhabiting saltwater, albeit rarely (e.g., Grigg *et al.* 1998, Grigg & Kirshner 2015). Therefore, all extant crocodylians are capable of traversing saltwater environments, including extant alligatorids to a more limited degree, despite their lack of specialized osmoregulatory adaptations.

Inferring the presence of salt-excreting glands among Crocodylia is not possible from fossilized skeletal material, as these glands are soft-tissue structures located on the surface of the tongue. Additionally, mekosuchine fossils are not known from coastal (except for the insular South West Pacific taxa) or marine deposits that could indirectly offer more credence to the potential osmoregulatory capabilities of these crocodylians. Salisbury *et al.* (2010) suggested that the insular species of *Mekosuchus* may have been saltwater tolerant, based on the lack of permanent freshwater rivers and lakes on New Caledonia during the Quaternary. However, if species of *Mekosuchus* were more terrestrial than extant crocodylians, then the lack of permanent freshwater bodies may not have played a key role in the lives of these animals. It is currently unclear when and how mekosuchines arrived in New Caledonia, Vanuatu and Fiji, considering that New Caledonia and Vanuatu were inhabited by the small-bodied and likely terrestrial species of *Mekosuchus*. Willis (2006) suggested rafting as a possible explanation as to how *Mekosuchus* spp. may have reached New Caledonia and Vanuatu. However, if rafting was not involved in the mekosuchine colonization of New Caledonia, Vanuatu and Fiji, then some degree of marine voyage combined with potential ‘island hopping’ seems probable in this alternative scenario. Although probably terrestrial, there are no apparent morphological features in the species of *Mekosuchus* that would have prevented them from being capable swimmers (Scanlon 2014). Regardless, the ancestral Australian mekosuchines may have resembled a plesiomorphic platyrostral crocodylian with a semi-aquatic palaeoecology akin to *Kambara* spp., rather than morphologically derived and terrestrial taxa like *Mekosuchus* spp.

It is plausible that at least the ancestral mekosuchines might have been saltwater tolerant to some degree, based on the potential palaeogeographical hypothesis presented here and by Rio & Mannion (2021). Alternatively, mekosuchines may have arrived in Australia by terrestrial dispersal throughout Asia into Europe, then the Americas, or from

Asia directly to the Americas; then, a possible land route may have been taken from South America *via* Antarctica, facilitating an entrance into Australia from the south (Rio & Mannion 2021). However, the latter hypothesis appears less likely due to the absence of fossil evidence of potential mekosuchines from anywhere in the Americas or Antarctica. Therefore, a more direct entrance from Asia into Australia (or, perhaps a route from Asia to the Indian subcontinent, and finally into Australia) during the Late Cretaceous–early Paleogene is a more parsimonious explanation. If so, then mekosuchines would not have been the only Australian crocodylians with Asian origins. Australia’s gavialoids (*Gu. maunala* and *H. camfieldensis*) and species of *Crocodylus* most likely entered Australia *via* southeast Asia and Wallacea as well (Ristevski *et al.* 2021), although at least in the case of *Crocodylus* spp. and perhaps the gavialoids, their arrival happened during the Neogene when the geographic separation between Asia and Australia was similar to that of today. Other reptile groups in Australia also have Asian origins that date back to the early Paleogene, such as egeriine skinks (Thorn *et al.* 2021a), sphenomorphine skinks (Rabosky *et al.* 2007), agamid lizards (Hugall *et al.* 2008), pythons, and elapid snakes (Sanders & Lee 2008).

Palaeodiversity patterns, ghost lineages, and gaps in the fossil record

Australasia is a globally important region for crocodyliform palaeontology and understanding the evolution of this group. Because continental Australia is the largest landmass in Australasia, it is no surprise that most known fossils have been discovered there (Fig. 2). At present, there are 30 recognized species from the Cenozoic of Australia, although some of them have uncertain taxonomic referrals (‘Runcorn taxon’, ‘Geebung taxon’, *Paludirex?* sp. nov.). Regardless of their generic and/or specific assignments, the recognition of these individual taxa contributes towards a more complete comprehension of the crocodylian taxonomic diversity throughout the Cenozoic of the continent.

Based on the currently known fossil taxa, Australia had a relatively low taxonomic diversity of crocodyliforms during the Eocene, with only one named genus and four species (if the ‘Runcorn taxon’ and ‘Geebung taxon’ represent new genera, it would indicate three genera and six species). Such low taxonomic diversity of crocodylians (and indeed crocodyliforms) from Australia’s Eocene contrasts with the then global trend of relatively high crocodyliform taxonomic diversity (Brochu 2003, Mannion *et al.* 2019, De Celis *et al.* 2020). The rather rich crocodyliform taxonomic diversity during the Eocene, and later again during the Miocene, is thought to be a result of global temperature maxima (Brochu 2003). However, a major diversification within Mekosuchinae in Australia is strongly suggested to have occurred sometime during the early–middle Eocene. The late Oligocene marks a notable increase in diversity, with six genera and six known species. The Miocene fossil record also attests to a high taxonomic diversity of crocodylians in Australia during the Cenozoic, with six genera and eight

species (although the Miocene material is known from only three localities: Riversleigh in Queensland, and Bullock Creek and Alcoota in the Northern Territory). This peak in taxonomic diversity during the Miocene is consistent with global diversity trends of Crocodylia during this epoch (Brochu 2003, Mannion *et al.* 2019, De Celis *et al.* 2020). The known Pliocene record reveals at least five genera and five species (or six genera and six species if *Gunggamarandu maunala* is considered Pliocene in age). The currently known record from the Pleistocene demonstrates the presence of four genera and five species (or five genera and six species, if *Gunggamarandu maunala* is considered Pleistocene in age). Future discoveries and studies will help refine and clarify the taxonomic composition of the group during the Cenozoic. Nevertheless, certain diversity patterns may be inferred based on current data.

The origin of Mekosuchinae is estimated to be no later than the early Paleocene (Danian, ~66–61.6 Ma), although the first definitive fossil evidence of the group in Australia (species of *Kambara*) is known from the early Eocene (Ypresian, at least ~56 Ma; Willis *et al.* 1993, Salisbury & Willis 1996). If Orientalosuchina is part of Mekosuchinae, then the group originated sometime in the Cretaceous. The next known record of Mekosuchinae in Australia is from the late Oligocene (Chattian, ~25 Ma), and by this point there is a substantial increase in both generic and specific diversity, where nearly all known Australian mekosuchine genera are represented. The ancestors of all Australian mekosuchines, except for species of *Kambara*, likely evolved no later than the middle Eocene; however, there is no known fossil record of any named Australian mekosuchine taxon prior to the Oligocene except for *Kambara*. Conversely, there is no evidence of *Kambara* after the end of the Eocene. There are no known taxa from earlier during the Oligocene either (Rupelian). Thus, there are obvious gaps in the fossil record for nearly all mekosuchines, stretching for more than 30 million years, including the morphologically derived Mekosuchini, such as the altirostral ziphodonts (e.g., *Quinkana* spp.) and the small-bodied terrestrial taxa (e.g., *Trilophosuchus rackhami* and *Mekosuchus* spp.). This suggests that a major mekosuchine radiation occurred sometime during the early–middle Eocene, and the fossil record is yet to reveal a wealth of material from this period.

The end of the Miocene witnessed the disappearance of the large-bodied generalist species in the genus *Baru*, the gavialoid *Harpacochampsia camfieldensis*, and the small-bodied terrestrial taxon *T. rackhami*. Furthermore, the extinction of species of *Trilophosuchus* and *Mekosuchus* from continental Australia marks the loss of small-bodied (<1 m in TL) crocodylian taxa on the mainland. The fossils of these small mekosuchines are known from inferred forest/rainforest palaeoenvironments of the Riversleigh World Heritage Area (Archer *et al.* 2000, 2006). Therefore, it is plausible that the continual northward drift of Australia/Sahul, married with climatic changes and the gradual aridification of the continent, may have contributed to the extinction of small-bodied mekosuchines in Australia.

Of course, the possibility that small-bodied mekosuchines survived in Australia after the Middle Miocene cannot yet be excluded, and their fossils from Plio-Pleistocene deposits may await discovery. The Pliocene records the first appearances of the gavialoid *Gu. maunala*, species of *Crocodylus* in Australia, and the mekosuchines *Kalthifrons aurivellensis* and *Paludirex vincenti*. If *Gu. maunala* is indeed more closely related to Eocene taxa from Europe, then there is a substantial ghost lineage between these gavialoids (Ristevski *et al.* 2021). Likewise, *Paludirex* has a ghost lineage. Phylogenetic analyses recover *Paludirex* as the sister taxon to either *Baru*, the *Baru* + *Quinkana* clade (Figs 24, 25), *Quinkana*, or the ([*Trilophosuchus* + *Mekosuchus*] + *Quinkana*) clade (see Ristevski *et al.* 2023). All of these scenarios suggest a ~30-million-year long ghost lineage for *Paludirex* going back to the late Eocene (Priabonian, ~37.71–33.9 Ma, or perhaps late Lutetian, ~43 Ma). The genus *Quinkana* has the longest and most continuous fossil record on continental Australia, from the late Oligocene until the Late Pleistocene (Molnar 1982c, Willis 1997a). The genus *Mekosuchus* has the longest fossil record in Australasia, although there is a notable gap in the fossil record between the last known species of *Mekosuchus* from Australia (the Middle Miocene *Mekosuchus sanderi*) and the Late Pleistocene–Holocene *Mekosuchus inexpectatus* from New Caledonia.

Australian record of Gavialoidea

There are some uncertainties regarding the exact phylogenetic positions of *Gunggamarandu maunala* and *Harpacochampsia camfieldensis* within Gavialoidea. Interestingly, none of the analyses performed here or in prior studies (Ristevski *et al.* 2021, 2023) recovered a sister-taxon relationship between the two Australian gavialoids, and separate analyses recovered *H. camfieldensis* in different positions within Gavialoidea (Figs 24, 25; see also Ristevski *et al.* 2023). The persistent recovery of *Gu. maunala* as a basal gavialoid and sister taxon to *Dollosuchooides densmorei* from the early Eocene of Europe is perhaps surprising. *Gunggamarandu maunala* shares several cranial features with *Do. densmorei*, such as the very large and widely spaced postoccipital processes of the supraoccipital (this condition also occurs in *Tomistoma schlegelii* [Müller 1838]), as well as the relatively large proportions of the supratemporal fenestrae and the (consequently) narrow intertemporal and posttemporal bars (the latter occur in many gavialoids: Ristevski *et al.* 2021). Another striking similarity that *Gu. maunala* shares with basal gavialoids from the Paleogene of Europe, specifically *Kentisuchus spenceri* (Buckland 1836), is the deep sub-triangular concavity on its cranial table. According to Rio & Mannion (2021), a similar cranial concavity also occurs in *To. schlegelii* and some caimanines (although not all *To. schlegelii* specimens possess a concave cranial table: e.g., TMM M-6342, JR pers. obs.). However, as stated by Ristevski *et al.* (2021), the holotype, and thus far only known specimen of *Gu. maunala* is limited to a partial braincase, which leaves most of the

craniomandibular and entire postcranial morphology of the species a mystery. It is possible that when more complete material of *Gu. maunala* comes to light, the revised character scores may point towards a more derived position within Gavialoidea. For now, the basal gavialoid position of *Gu. maunala* remains the only recovered phylogenetic placement.

The timing of gavialoid arrival in Australia is unclear, although, as noted by Ristevski *et al.* (2021), the group was already present on the continent by the Middle Miocene (as demonstrated by *H. camfieldensis*). The most plausible palaeobiogeographic scenario related to their arrival indicates an entrance from the north via southeast Asia and Wallacea as the likely route (Ristevski *et al.* 2021). If the phylogenetic results are correct in that *Gu. maunala* and *H. camfieldensis* do not form a monophyletic Australian gavialoid clade, then this would imply two independent arrivals of gavialoids into Australia. However, the taxonomic status and phylogenetic placement of '*Gavialis papuensis*' is currently unclear. If future studies determine that '*Gavialis papuensis*' is not closely related to either *Gu. maunala* or *H. camfieldensis*, then that would suggest there were three independent gavialoid arrivals in Australasia: two in continental Australia (*Gu. maunala* and *H. camfieldensis*), and one in northern Sahul ('*Gavialis papuensis*' in the Solomon Sea).

Conclusions

Australasia has a rich fossil record of crocodyliforms spanning from the Early Cretaceous to the Holocene. All Mesozoic crocodyliforms from the region are known from continental Australia, where only two genera are currently recognized, *Confractosuchus* and *Isisfordia*. Both of these taxa are either derived non-eusuchian neosuchians or basal eusuchians. Overall, the crocodyliform taxonomic diversity from Australia's Mesozoic is low when compared to the other major Gondwanan landmasses, particularly South America, which was dominated by notosuchian crocodyliforms during the Late Cretaceous. However, the perceived low taxonomic diversity during the Mesozoic of Australia is most likely a result of sampling biases. The presence of Susisuchidae in both Australia (*Isisfordia* spp.) and South America (*Susisuchus* spp.) attests to the crocodyliform interchange between these landmasses during the Cretaceous. Although non-neosuchian crocodyliforms are not yet recognized from Australasia, it is possible that their presence is awaiting future discovery.

Unlike the known record from the Mesozoic, the Cenozoic of Australasia is marked by more abundant taxonomic diversity. From the early Eocene until the Holocene, Australasia was dominated by members of the crocodylian clade Mekosuchinae, a taxonomically diverse group with an unambiguous fossil record from Australia, New Caledonia, Vanuatu, Fiji, and probably New Guinea. New Zealand/Aotearoa has a poor crocodylian fossil record that is known solely from the Miocene. Although its relationships are uncertain, it is possible that the New Zealand taxon/taxa may also be mekosuchine(s). In Australia,

mekosuchines evolved into several genera with some containing multiple species. Such taxonomic diversity contributed to the evolution of mekosuchines exemplified by different body sizes and exploitation of distinct trophic niches and palaeohabitats. This diversity is characterized by large (at least ~4 m in TL: e.g., *Paludirex vincenti*) to small-sized (<1 m in TL: e.g., *Trilophosuchus rackhami*) mekosuchines, with inferred semi-aquatic (e.g., *Kambara* spp., *Paludirex* spp.) to primarily (but perhaps not exclusively) terrestrial (e.g., *Mekosuchus* spp., *Quinkana* spp., *Trilophosuchus* spp.) palaeoecologies. Morphological diversity reflected in the snout shape is also notable among mekosuchines, including platyrostral mesorostrine (e.g., *Australosuchus clarkae*, *Kambara* spp.), platyrostral brevirostrine (e.g., *Paludirex* spp.), short altirostral (e.g., *Mekosuchus* spp., *T. rackhami*), as well as disparity of the dentition that includes ziphodonty (e.g., *Quinkana* spp.). Indeed, the ziphodont mekosuchines from Australia are the stratigraphically youngest ziphodont crocodyliforms in the world.

Mekosuchinae is not a subclade of Crocodylidae, as most of our phylogenetic results find the clade in a basal position within Crocodyloidea. However, based on our morphological comparisons and phylogenetic assessments, there are some indications that suggest a stem Longirostres placement for Mekosuchinae, which also includes Orientalosuchina. These results imply that mekosuchines originated in the Cretaceous of Asia and arrived in Australia from South East Asia sometime in the Late Cretaceous or Paleocene. Based on these results, *Jiangxisuchus nankangensis* from the Late Cretaceous (Maastrichtian) of China would be the oldest known mekosuchine. Under this hypothesis, Mekosuchinae would no longer be regarded as an Australasian endemic radiation, as members of this clade were present on continental Asia.

In addition to mekosuchines, Australasia was also home to gavialoids, whereas species of *Crocodylus* are the only extant crocodylians in the region. Two gavialoids are known from Australia: *Harpacochampsa camfieldensis* from the Middle Miocene, and *Gunggamarandu maunala* from the Pliocene or Pleistocene. Based on morphological comparisons and multiple phylogenetic analyses, *Gunggamarandu* and *Harpacochampsa* seem to be distantly related, which indicates that there was more than one wave of gavialoid colonization of Australia. The taxonomically enigmatic '*Gavialis papuensis*' from Muyua in the Solomon Sea is known from highly fragmentary material and needs revision. Four species of *Crocodylus*, three of which are endemic to Australasia, are the only surviving crocodylians in the region. In Australia, *Crocodylus* has a relatively poor fossil record that points towards a rather complex evolutionary history on the continent, one marked by multiple waves of immigrations and colonization and the presence of three species within this genus, from the Pliocene to present.

Evolutionary inferences from the phylogenetic analyses imply that a major diversification of Mekosuchinae likely occurred sometime in the Eocene which, if correct, would suggest a diversity peak for crocodylians in Australia that would be consistent with the global diversity trends from

the Eocene. A notable lack of fossils from the late Eocene–late Oligocene of Australia is not exclusive to crocodylians, as Archer *et al.* (1999) referred to this interval as one of Australia’s ‘Dark Ages’ for fossil mammals. This is partially a consequence of the lack of additional fossil-bearing localities from this time interval. With these observations we identify significant gaps in the fossil record, and we predict that many discoveries are yet to be made from Eocene–late Oligocene deposits.

The disappearance of mekosuchines on mainland Australia coincides with the megafaunal extinction from the Late Pleistocene, and may correlate with climatic changes, habitat degradation and/or trophic collapse as a consequence of the loss of megafaunal prey species. However, why and how species of *Crocodylus* managed to survive where mekosuchines did not is unclear. Perhaps mekosuchines were restricted to habitats and preyed on megafauna that were more susceptible to climate change than the potentially more adaptable *C. johnstoni* and *C. porosus* (with the latter having no unambiguous fossil record). The last surviving mekosuchines from the South Pacific went extinct soon after human colonization of their home islands. Although definitive evidence of human extirpation of these mekosuchines is currently lacking, at least some degree of anthropogenic involvement, be it direct (e.g., exploitation for food), indirect (e.g., habitat alteration, and/or introduction of invasive species) or a combination of both may have factored in their demise.

Dedication (by PMAW)

It was late 1985 when Jeanette Muirhead and I had just finished our undergraduate studies at Sydney University, both of us completing a double major in Zoology and Geology. We both wanted to go on to do further work in vertebrate palaeontology, a subject not offered at Sydney University at that time, so it was suggested that we go and talk to Michael Archer at the University of New South Wales (UNSW), Sydney. His welcoming words were, “Finally, Sydney University has produced something useful!” I wanted to look at dinosaurs, but Mike said he didn’t have any to study. He did have lots of crocodiles that needed attention, would I be interested? Thus started my research career in crocodylian palaeontology. I was soon followed by John Scanlon, also from Sydney University, who went on to study fossil snakes under Mike. Then another academic refugee from Sydney, Steve Salisbury, also came to Mike and started work on fossil crocodylians.

Steve and I worked closely with Ralph Molnar, then at the Queensland Museum, in our early works on crocodylians and Steve went on to gain an academic post at the University of Queensland where his research interests broadened to include dinosaurs. In that position, Steve has taken on several doctoral students, some working on crocodylians including Jorgo Ristevski.

Meanwhile, back at UNSW, Mike also took on many PhD candidates including Michael Stein for further work on the crocodylians of Riversleigh. This is how a mere

mammalogist supported the flourishing studies into Australasian crocodylians. Directly or indirectly, Mike Archer is responsible for the start of the academic careers of four of the eight authors of this paper. Clearly the state of crocodylian palaeontology in Australia would not be as mature as it is today without his support and guidance in the careers of so many of us.

This paper is part of a special issue dedicated to Michael Archer.

Acknowledgements

For specimen access at various institutions in Australia, we are grateful to the staff at the AM, AAOD, Chinchilla Museum, MAGNT, QM, and SAMA. Scott Hocknull (QM) provided CT data for QM F1752. Susannah Maidment (NHMUK) contributed photographs. Tobias Massonne, Xiao-Chun Wu and Hsi-yin Shan shared useful information. Finally, we express our gratitude to Pedro Godoy, an anonymous reviewer and the Guest Editors and Editorial Board of *Alcheringa* for their comments and improvements on our manuscript.

Disclosure statement

No potential conflict of interest is reported by the author(s).

Funding

This study was supported by a University of Queensland International Postgraduate Scholarship to JR.

ORCID

Jorgo Ristevski  <http://orcid.org/0000-0001-9006-219X>
 Adam M. Yates  <http://orcid.org/0000-0003-3568-2585>
 Matt A. White  <http://orcid.org/0000-0002-4765-0356>
 Lachlan J. Hart  <http://orcid.org/0000-0002-1994-797X>
 Michael D. Stein  <http://orcid.org/0000-0002-0816-6326>
 Gilbert J. Price  <http://orcid.org/0000-0001-8406-4594>
 Steven W. Salisbury  <http://orcid.org/0000-0003-4097-8567>

Supplementary material

Supplemental data for this article can be accessed online at <https://doi.org/10.1080/03115518.2023.2201319>.

References

- AGASSIZ, L., 1849. Remarks on crocodiles of the green sand of New Jersey and on Atlantochelys. *Proceedings of the Academy of Natural Sciences of Philadelphia* 4, 169.
- AGNOLÍN, F.L., EZCURRA, M.D., PAIS, D.F. & SALISBURY, S.W., 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology* 8, 257–300.
- ANDERSON, I., 1999. Found: Fiji’s elusive giants. *New Scientist* 163, 14.
- ANDERSON, A., SAND, C., PETCHEY, F. & WORTHY, T.H., 2010. Faunal extinction and human habitation in New Caledonia: initial results and implications of new research at the Pindai Caves. *Journal of Pacific Archaeology* 1, 89–109.
- DE ANDRADE, M.B., EDMONDS, R., BENTON, M.J. & SCHOUTEN, R., 2011. A new Berriasiian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. *Zoological Journal of the Linnean Society* 163, S66–S108.

- ANDREWS, C.W., 1905. I.—Notes on some new Crocodylia from the Eocene of Egypt. *Geological Magazine* 2, 481–484.
- AOKI, R., 1988. Protruded toothed fossil crocodylian from the Solomon Islands – *Gavialis papuanus*. *Aquabiology* 10, 160.
- ARCHER, M., 1978. Quaternary vertebrate faunas from the Texas Caves of southeastern Queensland. *Memoirs of the Queensland Museum* 19, 61–109.
- ARCHER, M. & WADE, M., 1976. Results of the Ray E. Lemley expeditions, part 1. The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum* 17, 379–397.
- ARCHER, M., ARENA, R., BASSAROVA, M., BLACK, K., BRAMMALL, J., COOKE, B., CREASER, P., CROSBY, K., GILLESPIE, A., GODTHELP, H., GOTT, M., HAND, S.J., KEAR, B., KRIKIMANN, A., MACKNESS, B., MUIRHEAD, J., MUSSER, A., MYERS, T., PLEDGE, N., WANG, Y. & WROE, S., 1999. The evolutionary history and diversity of Australian mammals. *Australian Mammalogy* 21, 1–45.
- ARCHER, M., HAND, S.J. & GODTHELP, H., 2000. *Australia's Lost World: Riversleigh, World Heritage Site*. Reed New Holland, New Holland Publishers, 264 pp.
- ARCHER, M., ARENA, D. A., BASSAROVA, M., BECK, R.M.D., BLACK, K., BOLES, W.E., BREWER, P., COOKE, B.N., CROSBY, K., GILLESPIE, A., GODTHELP, H., HAND, S.J., KEAR, B.P., LOUYS, J., MORRELL, A., MUIRHEAD, J., ROBERTS, K.K., SCANLON, J.D., TRAVOUILLON, K.J. & WROE, S., 2006. Current status of species-level representation in faunas from selected fossil localities in the Riversleigh World Heritage Area, northwestern Queensland. *Alcheringa* 30, 1–17.
- AZZARÀ, B., BOSCHIAN, G., BROCHU, C.A., DELFINO, M., IURINO, D.A., KIMAMBO, J.S., MANZI, G., MASAO, F.T., MENCONERO, S., NJAU, J.K. & CHERIN, M., 2021. A new cranium of *Crocodylus anthropophagus* from Olduvai Gorge, northern Tanzania. *Rivista Italiana di Paleontologia e Stratigrafia* 127, 275–295.
- BALOUET, J.C., 1984. Les étranges fossiles de Nouvelle-Calédonie. *La Recherche* 15, 390–392.
- BALOUET, J.C., 1989. New Caledonian crocodile (*Mekosuchus inexpectatus*). P. 36. In *Crocodyles and Alligators*. ROSS C.A. (consulting ed.), Golden Press, Sydney.
- BALOUET, J.C., 1991. The fossil vertebrate record of New Caledonia. In *Vertebrate Palaeontology of Australasia*. VICKERS-RICH P., MONAGHAN J. M., BAIRD, R. F. & RICH, T. H. eds., Monash University Publications Committee, Melbourne, Australia, 1381–1409.
- BALOUET, J.C. & BUFFETAUT, E., 1987. *Mekosuchus inexpectatus*, n. g., n. sp., Crocodylien nouveau de l'Holocène de Nouvelle Calédonie. *Comptes rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre* 304, 853–856.
- BELL, P.R., FANTI, F., HART, L.J., MILAN, L.A., CRAVEN, S.J., BROUGHAM, T. & SMITH, E., 2019. Revised geology, age, and vertebrate diversity of the dinosaur-bearing Griman Creek Formation (Cenomanian), Lightning Ridge, New South Wales, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 514, 655–671.
- BENTON, M.J. & CLARK, J.M., 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pp. 295–338. in BENTON, M.J. ed., *The Phylogeny and Classification of the Tetrapods, Vol. i: Amphibians, Reptiles, Birds*. Clarendon Press, Oxford.
- BERG, D.E., 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*?, aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* 52, 1–105.
- BROCHU, C.A., 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Journal of Vertebrate Palaeontology* 19, 9–100.
- BROCHU, C.A., 2001. Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation. *American Zoologist* 41, 564–585.
- BROCHU, C.A., 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences* 31, 357–397.
- BROCHU, C.A., 2006. A new miniature horned crocodile from the Quaternary of Aldabara Atoll, Western Indian Ocean. *Copeia* 2006, 149–158.2.0.CO;2]
- BROCHU, C.A., 2007a. Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zoological Journal of the Linnean Society* 150, 835–863.
- BROCHU, C.A., 2007b. Systematics and taxonomy of Eocene tomistomine crocodylians from Britain and northern Europe. *Palaeontology* 50, 917–928.
- BROCHU, C.A., 2012. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103, 521–550.
- BROCHU, C.A. & STORRS, G.W., 2012. A giant crocodile from the Plio-Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of *Crocodylus* in Africa. *Journal of Vertebrate Palaeontology* 32, 587–602.
- BROCHU, C.A., DE CELIS, A., ADAMS, A.J., DRUMHELLER, S.K., NESTLER, J.H., BENEFIT, B.R., GROSSMAN, A., KIRERA, F., LEHMANN, T., LIUTKUS-PIERCE, C., MANTHI, F.K., MCCROSSIN, M.L., MCNULTY, K.P. & NYABOKE JUMA, R., 2022. Giant dwarf crocodiles from the Miocene of Kenya and crocodylid faunal dynamics in the Late Cenozoic of East Africa. *The Anatomical Record* 305, –2729–2765.
- BUCHANAN, L.A., 2008. *The systematics, palaeobiology and palaeoecology of Kambara taraina sp. nov. from the Eocene Rundle Formation, Queensland*. Unpublished PhD thesis, Monash University, Melbourne, 340 pp.
- BUCHANAN, L.A., 2009. *Kambara taraina sp. nov.* (Crocodylia, Crocodyloidea), a new Eocene mekosuchine from Queensland, Australia, and a revision of the genus. *Journal of Vertebrate Palaeontology* 29, 473–486.
- BUCKLAND, W., 1836. *Geology and Mineralogy Considered with Reference to Natural Theology*. Pickering, London, 618 pp.
- BUFFETAUT, E., 1983. Sur la persistance tardive d'un Crocodylien archaïque dans le Pléistocène de l'Île des Pins (Nouvelle-Calédonie) et sa signification biogéographique. *Comptes rendus des séances de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers. Sciences de la Terre* 297, 89–92.
- BUSBY, A.B.I.I., 1986. New material of *Sebecus* cf. *huilensis* (Crocodylia: Sebecosuchidae) from the Miocene La Venta Formation of Colombia. *Journal of Vertebrate Palaeontology* 6, 20–27.
- BUSBY, A.B., 1995. The structural consequences of skull flattening in crocodylians. *Functional Morphology in Vertebrate Palaeontology* 1995, 173–192.
- CAMPBELL, B., PRICE, G.J., LOUYS, J. & MISZKIEWICZ, J.J., 2021. Crocodile tooth histology from a Pliocene deposit in Chinchilla, Queensland. *Proceedings of the Royal Society of Queensland* 129, 37–46.
- CHAZEAU, J., 1993. Research on New Caledonian terrestrial fauna: achievements and prospects. *Biodiversity Letters* 1, 123–129.
- CHIOTAKIS, C., 2018. *Pliocene crocodylians of Chinchilla: identification using dental morphometrics*. Unpublished MRes thesis, Queensland University of Technology, Brisbane, 132 pp.
- CHIOTAKIS, C., 2019. Determining Australian Plio-Pleistocene crocodylian diversity using three dimensional morphometrics of dental and osteoderm remains. *Journal of Vertebrate Palaeontology, Program and Abstracts* 2019, 79.
- CLARK, J.M. & NORELL, M.A., 1992. The Early Cretaceous crocodylomorph *Hylaeochampsia vectiana* from the Wealden of the Isle of Wight. *American Museum Novitates* 3032, 1–19.
- CLARKE, W.B., 1869. *Dinornis* an Australian genus. *Geological Magazine* 6, 383–384.
- COOK, A.G., BRYAN, S.E. & DRAPER, J.J., 2013. Post-orogenic Mesozoic basins and magmatism. In *Geology of Queensland*. JELL, P., ed. Geological Survey of Queensland, Australia, 515–575.
- COPE, E.D., 1861. Recent species of Emydosaurian reptiles represented in the Museum of the Academy. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1860, 549–551.
- COSHELL, L., 1986. *The sedimentology of the Rundle oil shale deposit*. Unpublished PhD thesis, University of New South Wales, Sydney, 304 pp.
- COSETTE, A.P., ADAMS, A.J., DRUMHELLER, S.K., NESTLER, J.H., BENEFIT, B.R., MCCROSSIN, M.L., MANTHI, F.K., JUMA, R.N. & BROCHU, C.A.,

2020. A new crocodylid from the middle Miocene of Kenya and the timing of crocodylian faunal change in the late Cenozoic of Africa. *Journal of Palaeontology* 94, 1165–1179.
- COTT, H.B., 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *The Transactions of the Zoological Society of London* 29, 211–356.
- CUVIER, G.L., 1807. Sur les différentes espèces de crocodiles vivans et sur leurs caractères distinctifs. *Annales du Muséum National d'Histoire Naturelle* 10, 8–86.
- DAINTREE, R., 1872. Notes on the geology of the Colony of Queensland: with an appendix, containing description of the fossils, by R. Etheridge, Esq., F. R. S., F. G. S., palaeontologist on the Geological Survey of Great Britain, and W. Carruthers, Esq., F. R. S., F. G. S., Keeper of the Botanical Department in the British Museum. *Quarterly Journal of the Geological Society* 28, 271–317.
- DAL SASSO, C., PASINI, G., FLEURY, G. & MAGANUCO, S., 2017. *Razanandrongobe sakalavae*, a gigantic mesoeucrocodylian from the Middle Jurassic of Madagascar, is the oldest known notosuchian. *PeerJ* 5, e3481.
- DAUDIN, F.M., 1802. *Histoire Naturelle, Générale et Particulière des Reptiles; ouvrage faisant suite à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon; et rédigée par C. S. Sonnini, membre de plusieurs sociétés savantes. Vol. 2.* F. Dufart, Paris [1802], 432 pp.
- DAVIS, A.C. & ARCHER, M., 1997. *Palorchestes azael* (Mammalia, Palorchestidae) from the late Pleistocene Terrace Site Local Fauna, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41, 315–320.
- DE CELIS, A., NARVÁEZ, I. & ORTEGA, F., 2020. Spatiotemporal palaeodiversity patterns of modern crocodiles (Crocodyliformes: Eusuchia). *Zoological Journal of the Linnean Society* 189, 635–656.
- DE LA FUENTE, M.S., STERLI, J. & MANIEL, I., 2014. Meiolaniforms: An extinct lineage of turtles of Gondwanan origin. In *Origin, Evolution and Biogeographic History of South American Turtles*. Springer Earth System Sciences. Springer, Cham, 133–142.
- DE VIS, C.W., 1886. On remains of an extinct saurian. *The Proceedings of the Royal Society of Queensland* 2, 181–191.
- DE VIS, C.W., 1905. Fossil vertebrates from New Guinea. *Annals of the Queensland Museum* 6, 26–31.
- DELFINO, M. & DE VOS, J., 2010. A revision of the Dubois crocodylians, *Gavialis bengawanicus* and *Crocodylus ossifragus*, from the Pleistocene *Homo erectus* beds of Java. *Journal of Vertebrate Palaeontology* 30, 427–441.
- DODSON, J., FULLAGAR, R., FURBY, J., JONES, R. & PROSSER, I., 1993. Humans and megafauna in a late Pleistocene environment from Cuddie Springs, north western New South Wales. *Archaeology in Oceania* 28, 94–99.
- DRUMHELLER, S.K. & WILBERG, E.W., 2020. A synthetic approach for assessing the interplay of form and function in the crocodyliiform snout. *Zoological Journal of the Linnean Society* 188, 507–521.
- DUBOIS, E., 1908. Das Geologische alter der Kendeng-oder Trinilfauna. *Tijdschrift van het Koninklijk Nederlandsch Aardrijkskundig Genootschap, series 2*, 1235–1270.
- EFRON, B., 1979. Bootstrap methods: another look at the jackknife. *The Annals of Statistics* 7, 1–26.
- ERICKSON, B.R., 1976. Osteology of the early eusuchian crocodile *Leidyosuchus formidabilis*, sp. nov. *Monographs of the Science Museum of Minnesota* 2, 1–61.
- ETHERIDGE, R., 1917. Reptilian notes: *Megalania prisca*, Owen, and *Notiosaurus dentatus*, Owen; lacertilian dermal armour; opalized remains from Lightning Ridge. *Proceedings of the Royal Society of Victoria* 29, 127–133.
- FARRIS, J.S., 1989. The retention index and the rescaled consistency index. *Cladistics: The International Journal of the Willi Hennig Society* 5, 417–419.
- FELSENSTEIN, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution; International Journal of Organic Evolution* 39, 783–791.
- FIGUEIREDO, R.G., MOREIRA, J.K.R., SARAIVA, A.A.F. & KELLNER, A.W.A., 2011. Description of a new specimen of *Susisuchus anatoceps* (Crocodylomorpha: Mesoeucrocodylia) from the Crato Formation (Santana Group) with comments on Neosuchia. *Zoological Journal of the Linnean Society* 163, S273–S288.
- FORTIER, D.C. & SCHULTZ, C.L., 2009. A new neosuchian crocodylomorph (Crocodyliformes, Mesoeucrocodylia) from the Early Cretaceous of north-east Brazil. *Palaeontology* 52, 991–1007.
- FISHER, D.C., 1981. Crocodylian scatology, microvertebrate concentrations, and enamel-less teeth. *Paleobiology* 7, 262–275.
- FITZINGER, L.J., 1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. *Nebst einer Verwandtschaftstafel und einem Verzeichnisse der Reptiliensammlung des K. K. Zoologischen Museum's zu Wien*. J. G. Heubner, Vienna, Austria, 66 pp.
- FLANNERY, T.F., 1984. Re-examination of the Quanbun Local Fauna, a Late Cenozoic vertebrate fauna from Western Australia. *Records of the Western Australian Museum* 11, 119–128.
- FLANNERY, T., 1990. Pleistocene faunal loss: implications of the after-shock for Australia's past and future. *Archaeology in Oceania* 25, 45–55.
- FLANNERY, T.F., 1993. The case of the missing meat eaters. *Natural History* 102, 40–45.
- FLANNERY, T.F., 1994. *The Future Eaters. An Ecological History of the Australasian Lands and People*. Chatswood, New South Wales, Reed Books, 423 pp.
- FOSTER, J.R. & LOCKLEY, M.G., 1997. Probable crocodylian tracks and traces from the Morrison Formation (Upper Jurassic) of eastern Utah. *Ichnos* 5, 121–129.
- FOURTAU, R., 1920. *Contribution à l'étude des vertèbres Miocènes de l'Égypte*. Egypt Survey Department, Cairo, 1–121.
- GAFFNEY, E.S., KOOL, L.K., BRINKMAN, D.B., RICH, T.H. & VICKERS-RICH, P., 1998. *Otwayemys*, a new cryptodiran turtle from the Early Cretaceous of Australia. *American Museum Novitates* 3233, 1–28.
- GMELIN, J.F., 1789. *Systema Naturae, per regna tria Naturae: secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tome 1*, pars II, 501–1032 Lyon (and Leipzig).
- GODOY, P.L., BENSON, R.B., BRONZATI, M. & BUTLER, R.J., 2019. The multi-peak adaptive landscape of crocodylomorph body size evolution. *BMC Evolutionary Biology* 19, 167.
- GOLOBOFF, P.A., 1993. Estimating character weights during tree search. *Cladistics: The International Journal of the Willi Hennig Society* 9, 83–91.
- GOLOBOFF, P.A. & CATALANO, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *The International Journal of the Willi Hennig Society* 32, 221–238.
- GOLOBOFF, P.A., FARRIS, J.S. & NIXON, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- GORTER, J.D. & NICOLL, R.S., 1978. Reptilian fossils from Windjana Gorge, Western Australia. *Journal of the Royal Society of Western Australia* 60, 97–104.
- GRAY, J.E., 1862. A synopsis of the species of alligators. *Annals and Magazine of Natural History* 10, 327–331.
- GRIGG, G. & KIRSHNER, D., 2015. *Biology and Evolution of Crocodylians*. Clayton South, Victoria, CSIRO Publishing, 649 pp.
- GRIGG, G.C., BEARD, L.A., MOULTON, T., QUEIROLO MELO, M.T. & TAPLIN, L.E., 1998. Osmoregulation by the broad-snouted caiman, *Caiman latirostris*, in estuarine habitat in southern Brazil. *Journal of Comparative Physiology B* 168, 445–452.
- HARSHMAN, J., HUDDLESTON, C.J., BOLLECK, J.P., PARSONS, T.J. & BRAUN, M.J., 2003. True and false gharials: a nuclear gene phylogeny of Crocodylia. *Systematic Biology* 52, 386–402.
- HART, L.J., 2020. Taxonomic clarifications concerning the crocodyliiform genus *Isisfordia*. *PeerJ* 8, e8630.
- HART, L.J., BELL, P.R., SMITH, E.T. & SALISBURY, S.W., 2019. *Isisfordia molnari* sp. nov., a new basal eusuchian from the mid-Cretaceous of Lightning Ridge, Australia. *PeerJ* 7, e7166.
- HART, L.J., BELL, P.R., SMITH, E.T., MITCHELL, D.R., BROUGHAM, T. & SALISBURY, S.W., 2021. A probable skeleton of *Isisfordia* (Crocodyliformes) and additional crocodyliiform remains from the

- Griman Creek Formation (Cenomanian, New South Wales, Australia). *Journal of Palaeontology* 95, 351–366.
- HAWKINS, S.C., 2015. *Human behavioural ecology, anthropogenic impact and subsistence change at the Teouma Lapita site, central Vanuatu, 3000-2500 BP*. Unpublished PhD thesis, The Australian National University, Canberra, 264 pp.
- HAY, O., 1930. *Second Bibliography and Catalogue of the Fossil Vertebrata of North America Volume 2*. Carnegie Institute, Washington, D.C. Publication 390.
- HECHT, M.K. & ARCHER, M., 1977. Presence of xiphodont crocodylians in the Tertiary and Pleistocene of Australia. *Alcheringa* 1, 383–385.
- HEKKALA, E., GATESY, J., NARECHANIA, A., MEREDITH, R., RUSSELLO, M., AARDEMA, M.L., JENSEN, E., MONTANARI, S., BROCHU, C., NORELL, M. & AMATO, G., 2021. Paleogenomics illuminates the evolutionary history of the extinct Holocene ‘horned’ crocodile of Madagascar, *Voay robustus*. *Communications Biology* 4, 505.
- HILL, D., PLAYFORD, G. & WOODS, J.T., 1970. *Cainozoic Fossils of Queensland*. Queensland Palaeontographical Society, Brisbane, 36 pp.
- HILLS, E.S., 1943. Tertiary fresh-water fishes and crocodylian remains from Gladstone and Duaringa. *Queensland. Memoirs of the Queensland Museum* 12, 96–100.
- HOCKNULL, S.A., 2009. *Late Cainozoic rainforest vertebrates from Australopapua: evolution, biogeography and extinction*. Unpublished PhD thesis, University of New South Wales, Sydney, 790 pp.
- HOCKNULL, S.A., RICHARD, L., ARNOLD, L.J., PIETSCH, T., JOANNES-BOYAU, R., PRICE, G.J., MOSS, P., WOOD, R., DOSSETO, A., LOUYS, J., OLLEY, J. & LAWRENCE, R.A., 2020. Extinction of eastern Sahul megafauna coincides with sustained environmental deterioration. *Nature Communications* 11, 2250.
- HOLDAWAY, R.N. & WORTHY, T.H., 2006. Evolution of New Zealand and its vertebrates. In *Evolution and Biogeography of Australasian Vertebrates*. MERRICK, J.R., ARCHER, M., HICKEY, G.M. & LEE, M.S.Y., eds. Australian Scientific Publishing, Oatlands, 111–128.
- HOLT, T.R. & SALISBURY, S.W., 2005. New crocodylian remains from Hiatus A Site (early Miocene), Riversleigh, north-western Queensland. *10th Conference on Australian Vertebrate Evolution, Palaeontology and Systematics. Naracoorte Caves World Heritage Area, South Australia, 29 March–2 April 2005*.
- HOLT, T.R., SALISBURY, S.W. & WILLIS, P.M.A., 2005. A new species of mekosuchine crocodylian from the middle Palaeogene Rundle Formation, central Queensland. *Memoirs of the Queensland Museum* 50, 207–218.
- HOLT, T.R., SALISBURY, S.W., WORTHY, T., SAND, C. & ANDERSON, A., 2007. New material of *Mekosuchus inexpectatus* (Crocodylia: Mekosuchinae) from the Quaternary of New Caledonia. Unpublished conference paper. Available on ResearchGate.
- HUGALL, A.F., FOSTER, R., HUTCHINSON, M. & LEE, M.S., 2008. Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. *Biological Journal of the Linnean Society* 93, 343–358.
- HUXLEY, T.H., 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodylia. *Quarterly Journal of the Geological Society* 31, 423–438.
- IJIMA, M. & KOBAYASHI, Y., 2019. Mosaic nature in the skeleton of East Asian crocodylians fills the morphological gap between “Tomistominae” and Gavialinae. *Cladistics: The International Journal of the Willi Hennig Society* 35, 623–632.
- IJIMA, M., QIAO, Y., LIN, W., PENG, Y., YONEDA, M. & LIU, J., 2022. An intermediate crocodylian linking two extant gharials from the Bronze Age of China and its human-induced extinction. *Proceedings of the Royal Society B* 289(1970), 20220085.
- INEICH, I., 2009. Bocourt’s Terrific Skink, *Phoboscincus bocourti* Brocchi, 1876 (Squamata, Scincidae, Lygosominae). In *Zoologia Neocaledonica 7: Biodiversity studies in New Caledonia*. GRANDCOLAS P., ed., Mémoires du Muséum national d’Histoire naturelle, 149–174.
- IRMIS, R.B., NESBITT, S.J. & SUES, H.-D., 2013. Early Crocodylomorpha. In *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin*. NESBITT, S.J., DESOJO J.B. & IRMIS, R.B., eds. Geological Society, Special Publications, London, 275–302.
- IRWIN, G., WORTHY, T.H., BEST, S., HAWKINS, S., CARPENTER, J. & MATARARABA, S., 2011. Further Investigations at the Naigani Lapita site (VL 21/5), Fiji: Excavation, Radiocarbon Dating and Palaeofaunal Extinction. *Journal of Pacific Archaeology* 2, 66–78.
- ISBERG, S., BALAGUERA-REINA, S.A. & ROSS, J.P., 2017. *Crocodylus johnstoni*. *The IUCN Red List of Threatened Species* 2017, e.T46589A3010118.
- JACK, R.L. & ETHERIDGE, R., JR., 1892. *The Geology and Palaeontology of Queensland and New Guinea*. Government Printer, Brisbane, 768 pp.
- JONES, O.A., 1927. The Tertiary deposits of the Moreton District, south-eastern Queensland. *The Proceedings of the Royal Society of Queensland* 38, 23–46.
- JOUVE, S., 2016. A new basal tomistomine (Crocodylia, Crocodyloidea) from Issel (Middle Eocene; France): palaeobiogeography of basal tomistomines and palaeogeographic consequences. *Zoological Journal of the Linnean Society* 177, 165–182.
- JOUVE, S., BARDET, N., JALIL, N.-E., SUBERBIOLA, X.P., BOUYA, B. & AMAGHZAZ, M., 2008. The oldest African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous-Tertiary boundary. *Journal of Vertebrate Palaeontology* 28, 409–421.
- JOUVE, S., BOUYA, B., AMAGHZAZ, M. & MESLOUH, S., 2015. *Maroccosuchus zennaroi* (Crocodylia: Tomistominae) from the Eocene of Morocco: phylogenetic and palaeobiogeographical implications of the basal-most tomistomine. *Journal of Systematic Palaeontology* 13, 421–445.
- JOYCE, W.G., 2017. A review of the fossil record of basal Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 58, 65–113.
- KLEY, N., SERTICH, J., TURNER, A., KRAUSE, D., O’CONNOR, P. & GEORGI, J., 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Palaeontology* 30, 13–98.
- KLUGE, A.G. & FARRIS, J.S., 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18, 1–32.
- KREFFT, G., 1873. Remarks on Australian crocodyles and description of a new species. *Proceedings of the Zoological Society of London* 1873, 334–335.
- LADUKE, T.C., KRAUSE, D.W., SCANLON, J.D. & KLEY, N.J., 2010. A Late Cretaceous (Maastrichtian) snake assemblage from the Maevarano Formation, Mahajanga basin, Madagascar. *Journal of Vertebrate Palaeontology* 30, 109–138.
- LANGSTON, W., 1965. Fossil crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America. *University of California Publications in Geological Science* 52, 1–157.
- LAURENTI, J.N., 1768. *Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentatis Circa Venena et Antiodota Reptilium Austriacorum*. J. T. de Trattner, Vienna, 214. pp.
- LEE, M.S.Y. & YATES, A.M., 2018. Tip-dating and homoplasy: reconciling the shallow molecular divergences of modern gharials with their long fossil record. *Proceedings of the Royal Society B: Biological Sciences* 285, 20181071.
- LEES, T., 1986. Catalogue of type, figured and mentioned fossil fish, amphibians and reptiles held by the Queensland Museum. *Memoirs of the Queensland Museum* 22, 265–288.
- LEITE, K.J. & FORTIER, D.C., 2018. The palate and choanae structure of the *Susisuchus anatoceps* (Crocodyliformes, Eusuchia): phylogenetic implications. *PeerJ*, 6, e5372.
- LESLIE, A.J. & TAPLIN, L.E., 2001. Recent developments in osmoregulation in crocodylians. In *Crocodylian Biology and Evolution*. GRIGG, G., SEEBACHER, F. & FRANKLIN, C.E., eds. Surrey Beatty & Sons, Sydney, 265–279.
- LESSON, R.P., 1831. Reptiles. pp. 291–336, pls. 1–7. In *Voyage aux Indes-Orientales, par le Nord de l’Europe, les provinces du Caucase, la Georgie, l’Arménie, et la Perse, suivi de détails topographiques, statistiques et autres sur le Pegou, les îles de Java, de Maurice et de Bourbon, sur le cap-de-bonne-esperance et Sainte-Helen, pendant les années 1825, 1826, 1827, 1828 et 1829*. BELANGER, I.G.S. ed. Zoologie. A. Bertrand, Paris, xxxix + 535 pp.

- LI, C., WU, X.-C. & RUFOLO, S.J., 2019. A new crocodyloid (Eusuchia: Crocodylia) from the Upper Cretaceous of China. *Cretaceous Research* 94, 25–39.
- LONG, J.A., 2017. Why Australasian vertebrate animals are so unique—A palaeontological perspective. *General and Comparative Endocrinology* 244, 2–10.
- LONGMAN, H.A., 1924. Some Queensland fossil vertebrates. *Memoirs of the Queensland Museum* 8, 16–28.
- LONGMAN, H.A., 1925. A crocodylian fossil from Lansdowne Station. *Memoirs of the Queensland Museum* 8, 103–108.
- LONGMAN, H.A., 1928. A large jaw of *Pallimnarchus pollens*. *Memoirs of the Queensland Museum* 9, 158–159.
- LONGMAN, H.A., 1929. Palaeontological notes. *Memoirs of the Queensland Museum* 9, 247–251.
- LOUYS, J. & PRICE, G.J., 2015. The Chinchilla Local Fauna: An exceptionally rich and well-preserved Pliocene vertebrate assemblage from fluvial deposits of south-eastern Queensland, Australia. *Acta Palaeontologica Polonica* 60, 551–572.
- LYDEKKER, R., 1888. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part I.* London, Order of the Trustees, 309 pp.
- MACKNESS, B. & SUTTON, R., 2000. Possible evidence of intraspecific aggression in a Pliocene crocodile from north Queensland. *Alcheringa* 24, 55–62.
- MACKNESS, B.S., COOPER, J.E., WILKINSON, C. & WILKINSON, D., 2010. Palaeopathology of a crocodile femur from the Pliocene of eastern Australia. *Alcheringa* 34, 515–521.
- MANNION, P.D., BENSON, R.B., CARRANO, M.T., TENNANT, J.P., JUDD, J. & BUTLER, R.J., 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. *Nature Communications* 6, 8438.
- MANNION, P.D., CHIARENZA, A.A., GODOY, P.L. & CHEAH, Y.N., 2019. Spatiotemporal sampling patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact on diversity. *Palaeontology* 62, 615–637.
- MARKWICK, P.J., 1998. Crocodylian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology* 24, 470–497.
- MARTIN, J.E., 2019. The taxonomic content of the genus *Gavialis* from the Siwalik Hills of India and Pakistan. *Papers in Palaeontology* 5, 483–497.
- MARTIN, J.E. & LAUPRASERT, K., 2010. A new primitive alligatorine from the Eocene of Thailand: relevance of Asiatic members to the radiation of the group. *Zoological Journal of the Linnean Society* 158, 608–628.
- MARTIN, J.E., BUFFETAUT, E., NAKSRI, W., LAUPRASERT, K. & CLAUDE, J., 2012. *Gavialis* from the Pleistocene of Thailand and its relevance for drainage connections from India to Java. *PLoS ONE* 7, e44541.
- MASSONNE, T., VASILYAN, D., RABI, M. & BOHME, M., 2019. A new alligatoroid from the Eocene of Vietnam highlights an extinct Asian clade independent from extant *Alligator sinensis*. *PeerJ* 7, e7562.
- MATHER, E.K., TENNYSON, A.J., SCOFIELD, R.P., DE PIETRI, V.L., HAND, S.J., ARCHER, M., HANDLEY, W.D. & WORTHY, T.H., 2019. Flightless rails (Aves: Rallidae) from the early Miocene St Bathans Fauna, Otago, New Zealand. *Journal of Systematic Palaeontology* 17, 423–449.
- MCNAMARA, G.C., 1990. The Wyandotte Local Fauna: a new, dated, Pleistocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum* 28, 285–297.
- MCNAMARA, G.C., 1993. Cape Hillsborough: a dated Eocene-Oligocene vertebrate fossil site from Northeastern Queensland. CAVEPS '93; *Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics (Abstracts)*. Adelaide, 19–21 April, 1993.
- MEAD, J.I., STEADMAN, D.W., BEDFORD, S.H., BELL, C.J. & SPRIGGS, M., 2002. New extinct mekosuchine crocodile from Vanuatu, South Pacific. *Copeia* 2002, 632–641.2.0.CO;2
- MEGIRIAN, D., 1992. *Meiolania brevicollis* sp. nov. (Testudines: Meiolaniidae): a new horned turtle from the Australian Miocene. *Alcheringa* 16, 93–106.
- MEGIRIAN, D., 1994. A new species of *Quinkana* Molnar (Eusuchia: Crocodylidae) from the Miocene Camfield Beds of northern Australia. *The Beagle : Records of the Museums and Art Galleries of the Northern Territory* 11, 145–166.
- MEGIRIAN, D., MURRAY, P.F. & WILLIS, P., 1991. A new crocodile of the gavial ectomorph morphology from the Miocene of northern Australia. *The Beagle* 8, 135–157.
- MEGIRIAN, D., MURRAY, P.F. & WELLS, R., 1996. The late Miocene Ongeva Local Fauna of central Australia. *The Beagle* 13, 9–37.
- MEGIRIAN, D., MURRAY, P., SCHWARTZ, L. & VON DER BORCH, C., 2004. Late Oligocene Kangaroo Well Local Fauna from the Ulta Limestone (new name), and climate of the Miocene oscillation across central Australia. *Australian Journal of Earth Sciences* 51, 701–741.
- MELSTROM, K.M. & IRMIS, R.B., 2019. Repeated evolution of herbivorous crocodyliforms during the age of dinosaurs. *Current Biology* 29, 2389–2395.e3.
- MEREDITH, R.W., HEKKALA, E.R., AMATO, G. & GATESY, J., 2011. A phylogenetic hypothesis for *Crocodylus* (Crocodylia) based on mitochondrial DNA: evidence for a trans-Atlantic voyage from Africa to the New World. *Molecular Phylogenetics and Evolution* 60, 183–191.
- MILBERG, P. & TYRBERG, T., 1993. Naïve birds and noble savages—a review of man-caused prehistoric extinctions of island birds. *Ecography* 16, 229–250.
- MITTERMEIER, R.A., WERNER, T.B. & LEES, A., 1996. New Caledonia—a conservation imperative for an ancient land. *Oryx* 30, 104–112.
- MOLNAR, R.E., 1977. Crocodile with laterally compressed snout: first find in Australia. *Science (New York, N.Y.)* 197, 62–64.
- MOLNAR, R.E., 1978a. Age of the Chillagoe crocodile. *Search* 9, 156–158.
- MOLNAR, R.E., 1978b. The crocodile from Tea Tree Cave and ziphodont crocodiles in Australia. *Journal of the Sydney Speleological Society* 22, 3–10.
- MOLNAR, R.E., 1979. *Crocodylus porosus* from the Pliocene Allingham Formation of North Queensland. *Memoirs of the Queensland Museum* 19, 357–365.
- MOLNAR, R.E., 1980. Procoelous crocodile from Lower Cretaceous of Lightning Ridge. N.S.W. *Memoirs of the Queensland Museum* 20, 65–75.
- MOLNAR, R.E., 1982a. A longirostrine crocodylian from Murua (Woodlark), Solomon Sea. *Memoirs of the Queensland Museum* 20, 675–685.
- MOLNAR, R.E., 1982b. *Pallimnarchus* and other Cenozoic crocodiles in Queensland. *Memoirs of the Queensland Museum* 20, 657–673.
- MOLNAR, R.E., 1982c. Pleistocene ziphodont crocodylians of Queensland. *Records of the Australian Museum* 33, 803–834.
- MOLNAR, R.E., 1991. Fossil reptiles in Australia. Pp. 606–702. in VICKERS-RICH, P., MONAGHAN, J.M., BAIRD, R.F. & RICH, T.H. (eds.), *Vertebrate Palaeontology of Australasia*, Monash University Publications Committee, Melbourne, Australia.
- MOLNAR, R.E., 1993. Biogeography and phylogeny of the Crocodylia. In GLASBY, C.J., ROSS G.J.B., & BEESLEY P.L., eds., *Fauna of Australia, Volume 2A: Amphibia and Reptilia*. Australian Government Publishing Service, Canberra, 344–348.
- MOLNAR, R.E., 2004. *Dragons in the Dust: The Paleobiology of the Giant Monitor Lizard Megalania*. Indiana University Press, Bloomington, 210 pp.
- MOLNAR, R.E. & POLE, M., 1997. A Miocene crocodylian from New Zealand. *Alcheringa* 21, 65–70.
- MOLNAR, R.E. & WILLIS, P.M.A., 2001. New crocodyliform material from the Early Cretaceous Griman Creek Formation, at Lightning Ridge, New South Wales. In GRIGG, G., SEEBACHER, F., & FRANKLIN, C.E., eds. *Crocodylian Biology and Evolution*, Surrey Beatty & Sons, Sydney, 75–82.
- MOLNAR, R.E., WORTHY, T. & WILLIS, P.M.A., 2002. An extinct Pleistocene endemic mekosuchine crocodylian from Fiji. *Journal of Vertebrate Paleontology* 22, 612–628.
- MOLNAR, R.E., PRICE, G.J. & SOBBE, I.H., 2017. The role of large reptilian, especially ziphodont crocodylian, predators in Australian Pleistocene terrestrial tetrapod trophic systems. *Journal of Vertebrate Paleontology, Program and Abstracts* 2017, 165.
- MOOK, C.C., 1924. A new crocodylian from Mongolia. *American Museum Novitates* 117, 1–5.

- MOOK, C.C., 1940. A new fossil crocodylian from Mongolia. *American Museum Novitates* 1097, 1–3.
- MOOK, C.C., 1941. A new crocodylian from the Lance Formation. *American Museum Novitates* 1128, 1–5.
- MÜLLER, S., 1838. Waarnemingen over de Indische krokodillen en Beschrijving van eene nieuwe soort. *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie. Amsterdam and Leyden* 5, 1–27.
- MURRAY, P. & MEGIRIAN, D., 1992. Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory. *The Beagle* 9, 195–217.
- MURRAY, P.F. & VICKERS-RICH, P., 2004. *Magnificent Mihirungs: The Colossal Flightless Birds of the Australian Dreamtime*. Indiana University Press, Bloomington, 410 pp.
- MURRAY, P.F. & MEGIRIAN, D., 2006. The Pwerte Marnte Marnte Local Fauna: a new vertebrate assemblage of presumed Oligocene age from the Northern Territory of Australia. *Alcheringa* 30, 211–228.
- MURRAY, P., MEGIRIAN, D. & WELLS, R., 1993. *Kolopsis yperus* sp. nov. (Zygomaturinae, Marsupialia) from the Ongeva Local Fauna: New evidence for the age of the Alcoota fossil beds of Central Australia. *The Beagle* 10, 155–171.
- MURRAY, C.M., RUSSO, P., ZORRILLA, A. & MCMAHAN, C.D., 2019. Divergent morphology among populations of the New Guinea crocodile, *Crocodylus novaeguinae* (Schmidt, 1928): diagnosis of an independent lineage and description of a new species. *Copeia* 107, 517–523.
- NESBITT, N.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.
- NICHOLL, C.S., HUNT, E.S., OUARHACHE, D. & MANNION, P.D., 2021. A second peirosaurid crocodyliform from the mid-Cretaceous Kem Kem Group of Morocco and the diversity of Gondwanan notosuchians outside South America. *Royal Society Open Science* 8, 211254.
- NJAU, J.K. & BLUMENSCHINE, R.J., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. *Journal of Human Evolution* 50, 142–162.
- NORELL, M.A. & CLARK, J.M., 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 60, 115–128.
- NOVAS, F.E., AGNOLIN, F.L., EZCURRA, M.D., PORFIRI, J. & CANALE, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research* 45, 174–215.
- OAKS, J.R., 2011. A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *International Journal of Organic Evolution* 65, 3285–3297.
- OPPEL, M., 1811. *Die Ordnung, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. Munich, Lindauer, 87 pp.
- PAOLILLO, A. & LINARES, O.J., 2007. Nuevos cocodrilos Sebecosuchia del Cenozoico Suramericano (Mesosuchia: Crocodylia). *Paleobiologia Neotropical* 3, 1–25.
- PARAGNANI, C.P., POROPAT, S.F., VICKERS-RICH, P. & RICH, T.H., 2019. Australia's oldest and highest paleolatitude crocodylomorphs from the Lower Cretaceous Eumeralla Formation (upper Aptian–lower Albian) of Dinosaur Cove, Victoria. *Journal of Vertebrate Paleontology, Program and Abstracts 2019*, 165.
- PLANE, M.D., 1967. Stratigraphy and vertebrate fauna of the Otibanda Formation, New Guinea. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics of Australia* 86, 1–64.
- POL, D. & LEARDI, J.M., 2015. Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the cretaceous of Gondwana. In FERNÁNDEZ, M. & HERRERA, Y. eds. *Reptiles Extintos—Volumen en Homenaje a Zulma Gasparini*. Asociación Paleontológica Argentina, Buenos Aires, 172–186.
- POL, D., TURNER, A.H. & NORELL, M.A., 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. *Bulletin of the American Museum of Natural History* 324, 1–103.
- POLE, M., DOUGLAS, B. & MASON, G., 2003. The terrestrial Miocene biota of southern New Zealand. *Journal of the Royal Society of New Zealand* 33, 415–426.
- POROPAT, S.F., MARTIN, S.K., TOSOLINI, A.-M.P., WAGSTAFF, B.E., BEAN, L.B., KEAR, B.P., VICKERS-RICH, P. & RICH, T.H., 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. *Alcheringa* 42, 157–229.
- POROPAT, S.F., WHITE, M.A., ZIEGLER, T., PENTLAND, A.H., RIGBY, S.L., DUNCAN, R.J., SLOAN, T. & ELLIOTT, D.A., 2021. A diverse Late Cretaceous vertebrate tracksite from the Winton Formation of Queensland, Australia. *PeerJ* 9, e11544.
- PRASAD, G.V., VERMA, O., FLYNN, J.J. & GOSWAMI, A., 2013. A new Late Cretaceous vertebrate fauna from the Cauvery Basin, South India: implications for Gondwanan paleobiogeography. *Journal of Vertebrate Paleontology* 33, 1260–1268.
- PRICE, G.J., FENG, Y.X., ZHAO, J.X. & WEBB, G.E., 2013. Direct U–Th dating of vertebrate fossils with minimum sampling destruction and application to museum specimens. *Quaternary Geochronology* 18, 1–8.
- PRICE, G.J., CRAMB, J., LOUYS, J. & FENG, Y.-X., 2017. Palaeontology of northeastern Australian caves. *Proceedings of the 17th International Congress of Speleology* 1, 25–28.
- PRICE, G.J., LOUYS, J., SOBBE, I.H., RISTEVSKI, J. & MOLNAR, R.E., 2019. Ecological fallout and turnover in the diversity of Late Quaternary terrestrial predators of Australia. *Journal of Vertebrate Paleontology, Program and Abstracts 2019*, 173.
- RABOSKY, D.L., DONNELLAN, S.C., TALABA, A.L. & LOVETTE, I.J., 2007. Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society. Proceedings Biological Sciences* 274, 2915–2923.
- RAUHE, M. & ROSSMANN, T., 1995. News about fossil crocodiles from the Middle Eocene of Messel and Geiseltal, Germany. *Hallesches Jahrbuch für Geowissenschaften* 17, 81–92.
- RAUHE, M., FREY, E., “DINO”, PEMBERTON, D.S. & ROSSMANN, T., 1999. Fossil crocodylians from the late Miocene Baynunah Formation of the Emirate of Abu Dhabi, United Arab Emirates: osteology and palaeoecology. In WHYBROW, P. J. & HILL, A., eds. *Fossil Vertebrates of Arabia*. Yale University Press, New Haven and London, 163–185.
- RIEK, E.F., 1952. The fossil insects of the Tertiary Redbank Plains Series. Part 1: an outline of the fossil assemblage with descriptions of the fossil insects of the orders Mecoptera and Neuroptera. *University of Queensland Papers, Department of Geology* 4, 3–14.
- RIFF, D., ROMANO, P.S.R., OLIVEIRA, G.R. & AGUILERA, O.A., 2009. Neogene crocodile and turtle fauna in northern South America. In *Amazonia: Landscape and Species Evolution: A Look into the past*. HOORN, C. & WESSELIINGH, F.P., eds. John Wiley & Sons, Chichester, 259–280.
- RIO, J.P. & MANNION, P.D., 2021. Phylogenetic analysis of a new morphological dataset elucidates the evolutionary history of Crocodylia and resolves the long-standing gharial problem. *PeerJ* 9, e12094.
- RISTEVSKI, J., 2022a. Neuroanatomy of the mekosuchine crocodylian *Trilophosuchus rackhami* Willis, 1993. *Journal of Anatomy* 241, 981–1013.
- RISTEVSKI, J., 2022b. *New insights into the taxonomic diversity and evolution of crocodylians from the Cenozoic Era of Australia*. Unpublished PhD thesis, The University of Queensland, Brisbane, 931 pp.
- RISTEVSKI, J., 2022c. Inside the head of one of the smallest crocodylians: paleoecological insights from the neuromorphology of *Trilophosuchus rackhami*, and tracing the origins of Mekosuchinae. *Journal of Vertebrate Paleontology, Program and Abstracts 2022*, 283–284.
- RISTEVSKI, J., YOUNG, M.T., DE ANDRADE, M.B. & HASTINGS, A.K., 2018. A new species of *Anteophthalmosuchus* (Crocodylomorpha, Goniopholididae) from the Lower Cretaceous of the Isle of Wight, United Kingdom, and a review of the genus. *Cretaceous Research* 84, 340–383.
- RISTEVSKI, J., PRICE, G.J., SOBBE, I.H., MOLNAR, R.E., LOUYS, J., CRAMB, J., NGUYEN, A.D., ZHAO, J.-X., FENG, Y.-X. & BEIRNE, L., 2019. A new ziphodont eusuchian from the Pleistocene of Queensland, and

- implications for Australasia's ziphodont crocodylian diversity. *Journal of Vertebrate Paleontology, Program and Abstracts 2019*, 180.
- RISTEVSKI, J., YATES, A.M., PRICE, G.J., MOLNAR, R.E., WEISBECKER, V. & SALISBURY, S.W., 2020a. Australia's prehistoric 'swamp king': revision of the Plio-Pleistocene crocodylian genus *Pallimnarchus* de Vis, 1886. *PeerJ*, 8, e10466.
- RISTEVSKI, J., YATES, A. M., PRICE, G. J., MOLNAR, R. E., WEISBECKER, V. & SALISBURY, S. W., 2020b. Data from: Australia's prehistoric 'swamp king': revision of the Plio-Pleistocene crocodylian genus *Pallimnarchus* de Vis, 1886. *Dryad, Dataset*
- RISTEVSKI, J., PRICE, G.J., WEISBECKER, V. & SALISBURY, S.W., 2021. First record of a tomistomine crocodylian from Australia. *Scientific Reports* 11, 12158.
- RISTEVSKI, J., WEISBECKER, V., SCANLON, J.D., PRICE, G.J. & SALISBURY, S.W., 2023. Cranial anatomy of the mekosuchine crocodylian *Trilophosuchus rackhami* Willis, 1993. *Anatomical Record* 306, 239–297.
- ROSSMANN, T., 1998. Studien an känozoischen Krokodilen: 2. Taxonomische Revision der Familie Pristichampsidae Efimov (Crocodylia: Eusuchia). *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen* 210, 85–128.
- ROSSMANN, T., 1999. Studien an känozoischen Krokodilen: 1. Die paläoökologische Bedeutung des eusuchen Krokodils *Pristichampus rollinatus* (Gray) für die Fossilagerstätte Grube Messel. *Courier Forschungsinstitut Senckenberg* 216, 85–96.
- SALAS-GISMONDI, R., FLYNN, J.J., BABY, P., TEJADA-LARA, J.V., CLAUDE, J. & ANTOINE, P.-O., 2016. A new 13 million year old gavialoid crocodylian from proto-Amazonian mega-wetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *PLoS One* 11, e0152453.
- SALISBURY, S.W. & WILLIS, P.M.A., 1996. A new crocodylian from the Early Eocene of south-eastern Queensland and a preliminary investigation of the phylogenetic relationships of crocodyloids. *Alcheringa* 20, 179–226.
- SALISBURY, S.W., MOLNAR, R.E. & WILLIS, P.M.A., 1995. Fossil gavial from the Pleistocene of Darling Downs, southeastern Queensland. *Wellington Caves Quaternary Symposium*.
- SALISBURY, S.W., FREY, E., MARTILL, D.M. & BUCHY, M.C., 2003. A new crocodylian from the Lower Cretaceous Crato formation of north-eastern Brazil. *Palaeontographica Abteilung A* 270, 3–47.
- SALISBURY, S.W., MOLNAR, R.E., FREY, E. & WILLIS, P.M.A., 2006. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. *Proceedings of the Royal Society B: Biological Sciences* 273(1600), 2439–2448.
- SALISBURY, S.W., HOLT, T.R., WORTHY, T.H., SAND, C. & ANDERSON, A., 2010. New material of *Mekosuchus inexpectatus* (Crocodylia: Mekosuchinae) from the Late Quaternary of New Caledonia, and the phylogenetic relationships of Australian Cenozoic crocodylians. *Journal of Vertebrate Paleontology, Program and Abstracts 2019*, 155A.
- SALISBURY, S.W., TENNYSON, A.J.D., SCOFIELD, R.P., HAND, S.J., ARCHER, M., DE PIETRI, V.L., WORTHY, J.P., BARHAM, K. & WORTHY, T.H., 2017. The crocodylian fauna of the lower Miocene Bannockburn Formation of St Bathans, Central Otago, New Zealand. *CAVEPS '17; Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics (Abstracts)*. Queenstown, New Zealand, 01–07 October 2017.
- SANDERS, K.L. & LEE, M.S., 2008. Molecular evidence for a rapid late-Miocene radiation of Australasian venomous snakes (Elapidae, Colubroidea). *Molecular Phylogenetics and Evolution* 46, 1165–1173.
- SCANLON, J., 2006a. Hiatus A Site – Crocodiles and their prey in interesting times. *Riversleigh Notes: The Newsletter of the Riversleigh Society* 63, 1–5.
- SCANLON, J., 2006b. Skull of the large non-macrostromatan snake *Yurlungur* from the Australian Oligo-Miocene. *Nature* 439, 839–842.
- SCANLON, J.D., 2014. Giant terrestrial reptilian carnivores of Cenozoic Australia. Pp. 27–53. in GLEN, A.S. & DICKMAN, C.R. eds., *Carnivores of Australia: Past, Present and Future*. CSIRO Publishing, Collingwood, 448 pp.
- SCHMIDT, K.P., 1928. A new crocodile from New Guinea. *Zoological Series of the Field Museum of Natural History* 12, 175–181.
- SCHMIDT, K.P., 1935. A new crocodile from the Philippine Islands. *Zoological Series of the Field Museum of Natural History* 20, 67–70.
- SCHNEIDER, J.G., 1801. *Historiae amphibiorum naturalis et literariae. Fasciculus secundus continens Crocodilos, Scincos, Chamaesauras, Boas. Pseudoboas, Elapes, Angues, Amphisbaenas et Caecillas*. Friedrich Frommann, Jena, 365 pp.
- SCHWARZHANS, W., SCOFIELD, R.P., TENNYSON, A.J., WORTHY, J.P. & WORTHY, T.H., 2012. Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand. *Acta Palaeontologica Polonica* 57, 319–350.
- SERENO, P.C., LARSSON, H.C.E., SIDOR, C.A. & GADO, B., 2001. The giant crocodyliiform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294, 1516–1519.
- SHAN, H.-Y., WU, X.-C., SATO, T., CHENG, Y.-N. & RUFOLO, S., 2021. A new alligatoroid (Eusuchia, Crocodylia) from the Eocene of China and its implications for the relationships of Orientalosuchina. *Journal of Paleontology* 95, 1321–1339.
- SILL, W.D., 1970. Nota preliminar sobre un nuevo gavial del Plioceno de Venezuela y una discusión de los gaviales sudamericanos. *Ameghiniana* 7, 151–159.
- SLAVENKO, A., TALLOWIN, O.J.S., ITESCU, Y., RAIJA, P. & MEIRI, S., 2016. Late Quaternary reptile extinctions: size matters, insularity dominates. *Global Ecology and Biogeography* 25, 1308–1320.
- SMITH, N.D., MAKOVICKY, P.J., AGNOLIN, F.L., EZCURRA, M.D., PAIS, D.F. & SALISBURY, S.W., 2008. A Megaraptor-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous. *Proceedings of the Royal Society B: Biological Sciences* 275(1647), 2085–2093.
- SOBBE, I.H., PRICE, G.J. & KNEZOUR, R.A., 2013. A ziphodont crocodile from the late Pleistocene King Creek catchment, Queensland. *Memoirs of the Queensland Museum – Nature* 56, 601–606.
- SOLMU, G. & MANOLIS, C., 2019. *Crocodylus novaeguinae*. *The IUCN Red List of Threatened Species 2019*, e.T46591A3010398.
- STEIN, M., SALISBURY, S.W., HAND, S.J., ARCHER, M. & GODTHELP, H., 2012. Humeral morphology of the early Eocene mekosuchine crocodylian *Kambara* from the Tingamarra Local Fauna southeastern Queensland, Australia. *Alcheringa* 36, 473–486.
- STEIN, M., HAND, S.J. & ARCHER, M., 2015. Dwarfism and feeding behaviours in Oligo-Miocene crocodiles from Riversleigh, northwestern Queensland, Australia. *Acta Palaeontologica Polonica* 61, 135–142.
- STEIN, M., HAND, S.J. & ARCHER, M., 2016. A new crocodile displaying extreme constriction of the mandible, from the late Oligocene of Riversleigh, Australia. *Journal of Vertebrate Paleontology* 36, e1179041.
- STEIN, M.D., YATES, A., HAND, S.J. & ARCHER, M., 2017. Variation in the pelvic and pectoral girdles of Australian Oligo-Miocene mekosuchine crocodiles with implications for locomotion and habitus. *PeerJ*, 5, e3501.
- STEIN, M., HAND, S.J., ARCHER, M., WROE, S. & WILSON, L.A., 2020. Quantitatively assessing mekosuchine crocodile locomotion by geometric morphometric and finite element analysis of the forelimb. *PeerJ*, 8, e9349.
- STERLI, J. & DE LA FUENTE, M.S., 2011. Re-description and evolutionary remarks on the Patagonian horned turtle *Niolamia argentina* Ameghino, 1899 (Testudinata, Meiolaniidae). *Journal of Vertebrate Paleontology* 31, 1210–1229.
- STERLI, J., DE LA FUENTE, M.S. & KRAUSE, M., 2015. A new turtle from the Palaeogene of Patagonia (Argentina) sheds new light on the diversity and evolution of the bizarre clade of horned turtles (Meiolaniidae, Testudinata). *Zoological Journal of the Linnean Society* 174, 519–548.
- STIRTON, R.A., 1967. *The Alcoota Fauna, Central Australia: An Integrated Palaeontological and Geological Study* (No 87). Bureau of Mineral Resources, Geology and Geophysics. 187 pp.
- STIRTON, R.A., TEDFORD, R.H. & MILLER, A.H., 1961. Cenozoic stratigraphy and vertebrate paleontology of the Tirari desert, South Australia. *Records of the South Australian Museum* 14, 19–61.

- STIRTON, R.A., TEDFORD, R.H. & WOODBURNE, M.O., 1967. A new Tertiary formation and fauna from the Tirari Desert, South Australia. *Records of the South Australian Museum* 15, 427–462.
- STOCKDALE, M.T. & BENTON, M.J., 2021. Environmental drivers of body size evolution in crocodile-line archosaurs. *Communications Biology* 4, 38.
- SYME, C.E. & SALISBURY, S.W., 2018. Taphonomy of *Isisfordia duncani* specimens from the Lower Cretaceous (upper Albian) portion of the Winton Formation, Isisford, central-west Queensland. *Royal Society Open Science* 5, 171651.
- TAPLIN, L.E., 1988. Osmoregulation in crocodylians. *Biological Reviews of Reviews* 63, 333–377.
- TAPLIN, L.E., GRIGG, G.C., HARLOW, P., ELLIS, T.M. & DUNSON, W.A., 1982. Lingual salt glands in *Crocodylus acutus* and *C. johnstoni* and their absence from *Alligator mississippiensis* and *Caiman crocodylus*. *Journal of Comparative Physiology B* 149, 43–47.
- TAPLIN, L.E., GRIGG, G.C. & BEARD, L., 1985. Salt gland function in fresh water crocodylians: evidence for a marine phase in eusuchian evolution? In *Biology of Australasian Frogs and Reptiles*, GRIGG, G., SHINE, R., EHMANN, H. Surrey Beatty and Sons, Sydney, 403–410.
- THOMPSON, P., 1980. Report on investigation of Myrtle Vale and Redbank; two fossil bone sites: Darling River Weir No. 20 Northwest N. S. W. Report for N. S. W. National Parks and Wildlife Service.
- THORN, K.M., HUTCHINSON, M.N., LEE, M.S.Y., BROWN, N.J., CAMENS, A.B. & WORTHY, T.H., 2021a. A new species of *Proegernia* from the Namba Formation in South Australia and the early evolution and environment of Australian egeriine skinks. *Royal Society Open Science* 8, 201686.
- THORN, K.M., POROPAT, S.F., BELL, P.R., HOCKNULL, S.A., KEAR, B.P., PALCI, A., SALISBURY, S.W. & YATES, A.M., 2021b. Checklist of the fossil reptile and amphibian species of Australia. [<https://www.australasianpalaeontologists.org/databases>].
- TROXELL, E.L., 1925. The Bridger crocodylians. *American Journal of Science* s5-9, 5th Ser. 9, 29–72.
- TUCKER, R.T., ROBERTS, E.M., HU, Y., KEMP, A.I. & SALISBURY, S.W., 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. *Gondwana Research* 24, 767–779.
- TUCKER, R.T., ROBERTS, E.M., DARLINGTON, V. & SALISBURY, S.W., 2017. Investigating the stratigraphy and palaeoenvironments for a suite of newly discovered mid-Cretaceous vertebrate fossil-localities in the Winton Formation, Queensland, Australia. *Sedimentary Geology* 358, 210–229.
- TURNER, A.H., 2015. A Review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. *PLoS One* 10, e0118116.
- TURNER, A.H. & PRITCHARD, A.C., 2015. The monophyly of Suisuchidae (Crocodyliformes) and its phylogenetic placement in Neosuchia. *PeerJ* 3, e759.
- VÉLEZ-JUARBE, J., BROCHU, C.A. & SANTOS, H., 2007. A gharial from the Oligocene of Puerto Rico: transoceanic dispersal in the history of a non-marine reptile. *Proceedings of the Royal Society. Biological Sciences* 274, 1245–1254.
- VICKERS-RICH, P. & RICH, T.H., 1999. *Wildlife of Gondwana: Dinosaurs & Other Vertebrates from the Ancient Supercontinent*. Bloomington, Indianapolis, Indiana University Press. 304 pp.
- WAGSTAFF, B.E., GALLAGHER, S.J., HALL, W.M., KORASIDIS, V.A., RICH, T.H., SEGETS-VILLIERS, D.E. & VICKERS-RICH, P.A., 2020. Palynological-age determination of Early Cretaceous vertebrate-bearing beds along the south Victorian coast of Australia, with implications for the spore-pollen biostratigraphy of the region. *Alcheringa* 44, 460–474.
- WEBB, G.J.W., MANOLIS, C., BRIEN, M.L., BALAGUERA-REINA, S.A. & ISBERG, S., 2021. *Crocodylus porosus*. *The IUCN Red List of Threatened Species* 2021 e.T5668A3047556.
- WHEATLEY, P.V., 2010. *Understanding saltwater tolerance and marine resource use in the Crocodylia: a stable isotope approach*. Unpublished PhD thesis, University of California, Santa Cruz, 167 pp.
- WHETSTONE, K.N. & WHYBROW, P.J., 1983. A “cursorial” crocodylian from the Triassic of Lesotho (Basutoland), Southern Africa. *Occasional Papers of the University of Kansas Museum of Natural History* 106, 1–37.
- WHITE, M.A., BELL, P.R., CAMPIONE, N.E., SANSALONE, G., BROUGHAM, T., BEVITT, J.J., MOLNAR, R.E., COOK, A.G., WROE, S. & ELLIOTT, D.A., 2022. Abdominal contents reveal Cretaceous crocodyliforms ate dinosaurs. *Gondwana Research* 106, 281–302.
- WILBERG, E.W., TURNER, A.H. & BROCHU, C.A., 2019. Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. *Scientific Reports* 9, 514.
- WILLIS, P., 1987. A fish-eating crocodile from the South Pacific. In HAND S. & ARCHER M. eds., *The Antipodean Ark*. Angus and Robertson, Sydney, 35–37.
- WILLIS, P.M.A., 1993a. The Australian palaeoherpetological renaissance: a review of Australian palaeoherpetology, 1990–93. In LUNNEY, D. & AYERS, D. eds., *Herpetology in Australia: A Diverse Discipline*. Royal Zoological Society of New South Wales, Sydney, 17–34.
- WILLIS, P.M.A., 1993b. *Trilophosuchus rackhami* gen. et sp. nov., a new crocodylian from the early Miocene limestones of Riversleigh, north-western Queensland. *Journal of Vertebrate Paleontology* 13, 90–98.
- WILLIS, P.M.A., 1995. *Phylogenetic systematics of Australian crocodylians*. Unpublished PhD thesis, University of New South Wales, Sydney, 276 pp.
- WILLIS, P.M.A., 1997a. New crocodylians from the late Oligocene White Hunter Site, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41, 423–438.
- WILLIS, P.M.A., 1997b. Review of fossil crocodylians from Australasia. *Australian Zoologist* 30, 287–298.
- WILLIS, P.M.A., 2001. New crocodylian material from the Miocene of Riversleigh (northwestern Queensland, Australia). In GRIGG, G., SEEBACHER, F. & FRANKLIN, C.E. eds., *Crocodylian Biology and Evolution*, Surrey Beatty & Sons, Sydney, 64–74.
- WILLIS, P.M.A., 2006. Evolution and zoogeography of Australasian crocodylians. In MERRICK, J.R., ARCHER, M., HICKEY, G.M. & LEE, M.S.Y. eds. *Evolution and Biogeography of Australasian Vertebrates*, Australian Scientific Publishing, Oatlands, 331–348.
- WILLIS, P.M.A. & ARCHER, M., 1990. A Pleistocene longirostrine crocodylian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. *Memoirs of the Queensland Museum* 28, 159–163.
- WILLIS, P.M.A. & MACKNESS, B.S., 1996. *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the early Pliocene Bluff Downs local fauna, northern Australia with a revision of the genus. *Proceedings of the Linnean Society of New South Wales* 116, 143–151.
- WILLIS, P.M.A. & MOLNAR, R.E., 1991a. A longirostrine crocodile from the Early Tertiary of southeastern Queensland. *Alcheringa* 15, 229–233.
- WILLIS, P.M.A. & MOLNAR, R.E., 1991b. A new Middle Tertiary crocodile from Lake Palankarinna, South Australia. *Records of the South Australian Museum* 25, 39–55.
- WILLIS, P.M.A. & MOLNAR, R.E., 1997a. A review of the Plio–Pleistocene crocodylian genus *Pallimnarchus*. *Proceedings of the Linnean Society of New South Wales* 117, 223–242.
- WILLIS, P.M.A. & MOLNAR, R.E., 1997b. Identification of large reptilian teeth from Plio–Pleistocene deposits of Australia. *Journal and Proceedings of the Royal Society of New South Wales* 130, 79–92.
- WILLIS, P. & THOMAS, A., 2005. *Digging up Deep Time: Fossils, Dinosaurs and Megabeasts from Australia's Distant Past*. ABC Books for the Australian Broadcasting Corporation, Sydney, 294 pp.
- WILLIS, P.M.A., MOLNAR, R.E. & SCANLON, J.D., 1993. An early Eocene crocodylian from Murgon, Southeastern Queensland. *Kaupia* 3, 27–33.
- WILLIS, P., MURRAY, P. & MEGIRIAN, D., 1990. *Baru darrowi* gen. et sp. nov., a large broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in northern Australia. *Memoirs of the Queensland Museum* 29, 521–540.
- WOODBURNE, M.O., 1967. The Alcoota Fauna, central Australia. *Bulletin of the Bureau of Mineral Resources Geology and Geophysics, Australia* 87, 1–187.

- WOODHEAD, J., HAND, S.J., ARCHER, M., GRAHAM, I., SNIDERMAN, K., ARENA, D.A., BLACK, K.H., GODTHELP, H., CREASER, P. & PRICE, E., 2016. Developing a radiometrically-dated chronologic sequence for Neogene biotic change in Australia, from the Riversleigh World Heritage Area of Queensland. *Gondwana Research* 29, 153–167.
- WORTHY, T.H. & ANDERSON, A., 1999. Research on the caves of Viti Levu, Fiji, June 1997–October 1998, and their significance for palaeontology and archaeology. *Report to the Fiji Museum, ANH, RSPAS, ANU, Canberra, ACT 0200, Australia*, 30 pp.
- WORTHY, T.H., ANDERSON, A. & MOLNAR, R.E., 1999. Megafaunal expression in a land without mammals – the first fossil faunas from terrestrial deposits in Fiji. *Senckenbergiana Biologica* 79, 237–242.
- WORTHY, T.H., HAND, S.J., ARCHER, M. & TENNYSON, A.D., 2006. The St Bathans Fauna – first insight into Neogene terrestrial vertebrate faunas in New Zealand. *Geological Society of New Zealand Miscellaneous Publication* 121, 35–36.
- WORTHY, T.H., HAND, S.J., LEE, M.S., HUTCHINSON, M., TENNYSON, A.J.D., SCOFIELD, R.P., MARSHALL, B., WORTHY, J.P., NGUYEN, J.M., BOLES, W.E. & ARCHER, M., 2009. New Zealand's St Bathans Fauna: an update on its composition and relationships. In TREWICK, S., HILLIER, N. & COOPER, R. eds. *Geology & Genes IV*. Geological Society of New Zealand Miscellaneous Publication (126), Wellington, 40–43.
- WROE, S., 2002. A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their diversity: the myth of reptilian domination and its broader ramifications. *Australian Journal of Zoology* 50, 1–24.
- WU, X.-C., CHENG, Z.W. & RUSSELL, A.P., 2001. Cranial anatomy of a new crocodyliform (Archosauria: Crocodylomorpha) from the Lower Cretaceous of Song-Liao Plain, northeastern China. *Canadian Journal of Earth Sciences* 38, 1653–1663.
- YATES, A.M., 2017. The biochronology and palaeobiogeography of *Baru* (Crocodylia: Mekosuchinae) based on new specimens from the Northern Territory and Queensland, Australia. *PeerJ*, 5, e3458.
- YATES, A.M., 2019. The last 10 million years of Australian crocodylian history: a case of out with the old and in with the new. *Journal of Vertebrate Paleontology, Program and Abstracts* 2019, 222.
- YATES, A.M. & PLEDGE, N.S., 2017. A Pliocene mekosuchine (Eusuchia: Crocodylia) from the Lake Eyre Basin of South Australia. *Journal of Vertebrate Paleontology* 37, e1244540.
- YOUNG, C.C., 1964. New fossil crocodiles from China. *Vertebrata Palasiatica* 8, 189–208.
- YOUNG, C.C., 1982. A *Cenozoic Crocodile from Huaining, Anhui. Selected Works of Yang Zhongjian*. China: Academia Sinica, 47–48.
- YOUNG, M.T., HASTINGS, A.K., ALLAIN, R. & SMITH, T.J., 2016. Revision of the enigmatic crocodyliform *Elosuchus felixi* de Lapparent de Broin, 2002 from the Lower–Upper Cretaceous boundary of Niger: potential evidence for an early origin of the clade Dyrosauridae. *Zoological Journal of the Linnean Society* 179, 377–403.
- ZANNO, L.E., DRYMALA, S., NESBITT, S.J. & SCHNEIDER, V.P., 2015. Early crocodylomorph increases top tier predator diversity during rise of dinosaurs. *Scientific Reports* 5, 9276.