The Nomenclature and Type Material of *Crocodylus johnstoni* (Krefft, 1873)

GLENN M. SHEA,^{1,2*} CECILIE A. BEATSON¹ AND ROSS A. SADLIER¹

¹ Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

² Faculty of Veterinary Science, University of Sydney NSW 2006, Australia

glenn.shea@sydney.edu.au http://orcid.org/0000-0002-0052-4205

ABSTRACT. The previously recognised original description of Crocodilus johnsoni Krefft, 1873 in the Proceedings of the Zoological Society of London is antedated by several months by a newspaper article penned by Krefft, in which the species is named as Crocodilus johnsonii. The same article validates the name Tomistoma krefftii, previously considered a nomen nudum. Tomistoma krefftii is a junior objective synonym of Crocodilus australis Krefft, 1867, both based on a dried head collected by William Woods near Burketown, Queensland. Both of these names potentially imperil stability of nomenclature of Crocodylus johnstoni, but the latter name is a nomen protectum, and the emendation of johnsonii to johnstoni is to be maintained due to prevailing and current usage. Crocodilus australis Krefft, 1867, a nomen oblitum with respect to C. johnstoni, is further a senior homonym in the genus Crocodylus of Oophilus porosus var. australis Gray, 1867 (another previously overlooked name). Crocodilus australis Bravard, in Burmeister, 1885, a Miocene fossil species from South America, currently in Caiman, and Crocodylus porosus australis Deraniyagala, 1953. The type specimen of Crocodilus australis Krefft is lost, but a contemporaneous archival photograph of what is presumed to be the specimen has been located. The holotype of *Crocodilus johnsonii*, originally described as just a skin, is redefined to include both the mounted skin (now missing the head) and an accompanying skeleton (now missing a skull), both bearing corresponding damage from a bullet wound at the time of collection. Archival photographs of the entire mounted skin, corresponding to a photograph sent to John Gray at the British Museum by Krefft in 1873 and to a cast of the head sent to Gray the following year, provide evidence that the head was removed from the mounted skin for casting shortly after the description of the species, and subsequently lost. A justification is provided, based on historical documentation, for the often emended type locality of C. johnstoni from the original Cardwell to Cashmere, Queensland.

KEYWORDS. Crocodilia; Crocodylus johnstoni; Tomistoma krefftii; Crocodilus australis; nomenclature; nomen oblitum; holotype

SHEA, GLENN M., CECILIE A. BEATSON AND ROSS A. SADLIER. 2016. The nomenclature and type material of *Crocodylus johnstoni* (Krefft, 1873). *Records of the Australian Museum* 68(3): 81–98. http://dx.doi.org/10.3853/j.2201-4349.68.2016.1658 The Australian Freshwater Crocodile, *Crocodylus johnstoni* (Krefft, 1873a), is a widespread endemic tropical Australian crocodile. The nomenclature of this iconic species has been stable since its first description, other than a dispute over whether the species name should be spelt *johnsoni*, based on the original spelling of an error in the collector's name, or *johnstoni*, a correction made by Gray (1874) at the request of Krefft, on discovering his error (see, for example, Boulenger, 1889; Wermuth, 1953; Mertens & Wermuth, 1955, Wermuth & Mertens, 1961, 1977; Cogger *et al.*, 1983; King, 1989), a dispute most recently considered in detail and resolved by Tucker (2010). The species has been the subject of extensive study, some of which has been recently reviewed by Grigg & Kirschner (2015), who cite over 60 publications dealing explicitly with this species since 1975.

However, to date, there have been no detailed studies of the nomenclature and type material of this species to complement and support systematic catalogues of crocodilians and basic listings of the putative types. In this paper, we report the existence of two previously overlooked early synonyms for *Crocodilus johnstoni* and a description of this species that antedates the generally cited publication of the name, and consider the identity and status of the type material and type localities. For the purposes of this paper, we accept the arguments of Tucker (2010) and recognise the specific epithet for the species as the emended *johnstoni*, but in discussing descriptions, we use the original spelling given in each paper.

To avoid confusion, we also note here that nineteenth century authors generally used the generic name *Crocodilus* (e.g., Schneider, 1801; Gray, 1867, 1872; Boulenger, 1889; Cope, 1900), although the name is attributed to Laurenti (1768) who spelt it *Crocodylus*, and the correct original spelling of the generic name is now followed.

Krefft's description of Crocodilus johnsoni in the Proceedings of the Zoological Society of London

Krefft's (1873a) description of *Crocodilus johnsoni* in the *Proceedings of the Zoological Society of London* (hereafter referred to as *ZSL Proceedings*), which has generally been considered the original publication of the species name, bears the writing date of 31 December 1872 and a date of receipt of 17 February 1873. It was read at the meeting of the Zoological Society of 18 March, 1873, the third of six papers read at that meeting. The *ZSL Proceedings* for 1873 is printed in the form of 16 page signatures, numbered on the lower left of the first page of each signature, with Krefft's paper (appearing on pages 334–335) being part of signature number XXI, which begins on page 321 and ends on page 336. The dates of each signature are not recorded. However, Duncan (1937) notes that these pages were included in Part II (pp. 241–624), which was issued in August 1873.

Hence, the date of publication of Krefft (1873a) must be considered to be August 1873. The delay between writing and receipt of the paper reflects the time taken for mail to be shipped from Sydney to London in the era of sail. The further delay between receipt and reading, despite two other meetings of the society being held in that period (18 February and 4 March) presumably reflects the need for refereeing of the paper before formal acceptance and reading.

Krefft's paper opens by reporting that he sent a photograph of a crocodile skull to John Edward Gray, Keeper of Zoology at the British Museum, "a year or two ago", which Gray had considered to represent a new species that he proposed to call *Tomistoma krefftii*, a name which Krefft was unable to identify as being published. Krefft noted that the skull differed from the only described species of *Tomistoma*, *T. schlegelii*, in features of osteology and dentition.

Krefft then described Crocodilus johnsoni from "a fine and perfect skin of another Crocodile" (our emphasis) that he had received. Although it is not clear from Krefft's paper whether he regarded the earlier skull as representing the same species he described as Crocodilus johnsoni, it has generally been presumed that Gray's Tomistoma krefftii is an unpublished name introduced in the synonymy of C. johnsoni (e.g., Wermuth, 1953; Mertens & Wermuth, 1955; Wermuth & Mertens, 1961, 1977; Cogger et al., 1983) and hence unavailable for nomenclatural purposes. This argument is supported by the inclusion with Krefft's paper in the ZSL Proceedings of a letter from Gray, in which he suggests that the earlier photograph of a head is likely to be the same species for which he had proposed the name Tomistoma krefftii. However, as Krefft presumably had not seen Grav's letter at the time of writing his paper (Grav notes that he had been sent a photograph of the whole skin, with the request to communicate to the Society some comments on it), Krefft's extensive initial commentary on Tomistoma krefftii and his statement that the holotype of Crocodilus *johnsoni* was "another Crocodile" could be interpreted as the two names being applied to different species in Krefft's mind.

That this interpretation is correct is apparent from an article Krefft wrote for the Sydney newspaper, the *Sydney Mail and New South Wales Advertiser* (hereafter referred to as the *Sydney Mail*), published as part of a series by Krefft under the initial banner "The Natural History of New South Wales". This series was begun by Krefft in the issue of 4 March 1871, with the stated purpose of trying to counter a deficiency in the availability of works on the Australian fauna "by giving in the columns of the Sydney Mail a series of articles on our natural history, which, in course of time, will form a complete work on the subject" (Krefft, 1871), and continued until 23 January 1876, although the initial standard title for the series was dropped in favour of more specific titles reflecting the group of organisms being described in each article.

On 4 January 1873, just four days after writing his manuscript sent to the Zoological Society, over a month before that manuscript was received by the Society, two months before the manuscript was read by the Society, and eight months before it was published, an article by Krefft on Australian crocodiles appeared in his series in the *Sydney Mail*.

Krefft's description of Australian crocodiles in the *Sydney Mail*

Krefft's (1873b) article in the *Sydney Mail*, titled "Remarks on Australian Crocodiles", lists the species of crocodiles recorded from Australia, and provides a description of each. He lists four species:

- 1 Crocodilus porosus
- 2 Tomistoma Schlegelii
- 3 Tomistoma (?) Krefftii
- 4 Crocodilus Johnsonii

Each species is accompanied by a short diagnostic description. That Krefft at the time considered *Tomistoma krefftii* distinct from *Crocodilus johnsonii* is also apparent from his first statement under the latter species: "there must be at least three long-snouted crocodiles in northern Queensland, if the number of teeth is of consequence in classification." (These being *Tomistoma schlegelii*, *T. krefftii* and *C. johnsonii*—the record of *T. schlegelii* in Australia is presumably from the distribution statement "Australasia, Borneo" for that species by Gray, 1867, 1872, although this is not explicitly stated by Krefft).

This article has two consequences for nomenclature. Firstly, it antedates the generally recognised description of C. johnsoni by several months, and hence must be regarded nomenclaturally as the first description of the species. This has little nomenclatural effect, as the description of the species by Krefft in the Sydney Mail (1873b) largely parallels the description by Krefft in the ZSL Proceedings (1873a) in terms of the characters mentioned, although the exact words used differ in several places, and the type specimen is the same. That Krefft (1873b) uses C. johnsonii in the newspaper article and uses C. johnsoni in the ZSL Proceedings (1873a) is of little consequence-under the Code the two names are homonymous (Article 58.14 of the International Code of Zoological Nomenclature), although the -ii termination has priority, based on the discovery of the earlier description by Krefft (1873b).

The second consequence is that *Tomistoma krefftii* is validated as an available name in this paper, distinct from *C. johnsoni*. Krefft's account clearly states that *T. krefftii* differs from *T. schlegeli* in possessing 19–20 teeth in the upper dental arch and 15 in the lower dental arch (*vs* 20 and 18 respectively for *T. schlegeli*) and has the mandibular symphysis extending only to the sixth tooth (*vs* the fifteenth tooth for *T. schlegeli*). His use of a question mark in the generic assignment is explained by his commentary on the extent of the mandibular symphysis, where *Tomistoma* was diagnosed in the literature by the great extent of the symphysis ("not having the necessary literature at my disposal, I cannot decide whether this crocodile should be made into a new genus or not" he wrote).

Krefft noted that *Tomistoma krefftii* is "founded upon a skull which I received from a gentleman of northern Queensland. It was stated that the animal grew to a length of about five or six feet, and frequented the lagoons of the interior. Dr. J. E. Gray, of the British Museum, described it from a photograph sent to him". With Gray never having published his description of *T. krefftii*, the formal description of the species, and validation of the name with at least one purported diagnostic character not available to Gray, must be the description provided by Krefft (1873b), although Krefft attributed the name to Gray in that article. Hence, we refer to the validated publication of the name *Tomistoma krefftii* as by Gray as given in the newspaper article in the *Sydney Mail* by Krefft (1873b).

Who was the unnamed "gentleman of northern Queensland"? Further study of Australian newspaper archives, now readily available through the Australian Newspaper Digitisation Program, has uncovered an earlier article by Krefft (1867) that resolves this issue, but adds yet another nomenclatural twist.

Krefft's 1867 article in The Australasian

The 1867 article by Krefft, published in a Victorian newspaper on 27 July 1867, begins with a discussion of the application of the name alligator and crocodile with respect to *Crocodilus porosus*, which had often been referred to colloquially, but incorrectly, as an alligator. It then states:

"Besides this large species, the range of which extends as far as India, we have another smaller kind, for which I have proposed the name of *Crocodilus Australis*. This little crocodile has a much more slender snout, almost as slender as a gavial, and the production outwards at the end is scarcely perceptible; the bones of the head are less rugose, and the teeth not so conical as those of *C. porosus*; there are nineteen in the upper jaw and fifteen in the lower. *C. porosus* has eighteen and fifteen respectively.

"I am indebted to Mr. William Wood, who has lately returned from the Gulf of Carpentaria, for a skull of this new crocodile, which is ten inches in length, the whole animal being about four or five feet. Mr. Wood informs me that these reptiles are plentiful in all the lagoons and waterholes in the neighbourhood of the gulf, and that they never grow larger than about seven or eight feet in length."

The head/skull referred to by Krefft in 1867 is presumably the same as that of which a photograph was sent by Krefft to Gray "a year or two" before the description of *C. johnsoni* in 1873, and on which Gray based his manuscript name *T. krefftii*, but the article also creates and nomenclaturally validates another name for *C. johnstoni*—*Crocodilus Australis*—which antedates all others. It would appear that Krefft forgot that he had named the species *C. australis* when he sent the photograph to Gray a few years later.

What is the evidence that the skull Krefft described as Crocodilus australis in 1867 is the same specimen that Gray was sent a photograph of in 1871, and that served as the basis for the Svdnev Mail description (Krefft, 1873b) of Tomistoma krefftii? Krefft (1867) noted that William Wood, from whom he had obtained the skull, had "lately returned from the Gulf of Carpentaria". Hence, Krefft had only recently received that specimen by July 1867, when his description of Crocodilus Australis appeared. The skull/head for Tomistoma krefftii must have been received by the end of 1871. Hence, the 1867 acquisition date of the skull of Crocodilus Australis would be concordant with the time lapsed when Krefft (1873a) noted that he had sent a photograph of it to Gray "a year or two ago", and with the comment by Gray (1874) that Krefft had sent to him the photograph of the skull on which the manuscript name was based in 1871.

There is no evidence for any other Freshwater Crocodile being obtained by the Australian Museum between 1867 and 1871. Monthly lists of donations of specimens to the Australian Museum were published in the local press, particularly in the Sydney Morning Herald, during Krefft's tenure at the Australian Museum. Annual listings of donated specimens were also included in the Museum's Annual Reports. While the monthly lists published in the Sydney press are not complete for all months between 1867 and 1871, there is a reasonably complete record, complemented by the annual listings. The first record of donation of any crocodiles to the Museum post 1867 is the receipt of two specimens in March 1872, both identified as Crocodilus porosus: one donated by the owners of the schooner Spunkie, received from Captain Brown; the other a young individual donated by Thomas Spence (Krefft, 1872). The receipt of these specimens was so unusual that it prompted a note appended to the list for that month by Krefft (as "G.K.") commenting again on the difference between alligators and crocodiles, and noting that Gray had already 'described a "false gavial" from Australia as *Tomistoma Krefftii*.' Regardless, this use of the name Tomistoma Krefftii is a nomen nudum, but does further indicate that Gray had been sent the photograph of the head by Krefft, and that Krefft had received return correspondence on this proposed identification, by March 1872. That Krefft could no longer remember the name of the donor of the skull of Tomistoma krefftii by 1873, merely referring to "a gentleman of northern Queensland", also implies a date of collection closer to 1867 than 1873.

The existence of the name *Crocodilus australis* Krefft, 1867 potentially threatens the stability of nomenclature of the Australian Freshwater Crocodile, and further, it is a potential homonym of three other taxa.

The other three *australis* epithets among crocodiles

Augusto Bravard, an Argentine-based French paleontologist, compiled a monograph of the fossil fauna of the marine terraces of Parana, published among the official papers of the Argentine National Government in 1858, in which he erected the taxon *Crocodilus australis* for all non-longirostrine crocodiles in those deposits. The name was published again by Bravard (1860) in a catalogue of his collections privately printed in Paris (Langston, 1965; Bona *et al.*, 2013). Bravard died in the March 1861 earthquake in Mendoza, Argentina (Burmeister, 1885).

Both publications are rare, and we have not been able to trace original copies of them. However, German Burmeister reprinted Bravard's (1858) monograph in 1883, and we have used this version as representing the 1858 original publication.

Crocodilus australis in this sense was transferred to a new genus *Proalligator* by Ambrosetti (1887), to *Alligator* by Rovereto (1912), to *Jacaretinga* by de Saez (1928), to *Caiman* by Kälin (1936), back to *Proalligator* by Langston (1965) and most recently has returned to *Caiman*, where it is recognised as a distinct species (Bona *et al.*, 2013).

Patterson (1936) and Langston (1965) considered *Crocodilus australis* Bravard (1858) to be a *nomen* nudum, due to the description being insufficiently detailed to distinguish the species, and attributed the name to Burmeister (1885), who provided a more extended description and diagnosis while still attributing the name to Bravard. Bravard's (1858) description states "Dientes bien conservados, fragmentos del cráneo, de las placas dorsales de la coraza y una vertebra perfecta. De las placas duda mucha si son en verdad del cocodrilo; pueden ser tambien de pescados", or, loosely translated: "Well preserved teeth, fragments of skull, dorsal armor plates and a perfect vertebra. Of the plates, there is much doubt if they are really crocodile; they could also be fish". It is clear that this is merely a statement of the material collected, without diagnostic characters sufficient to validate the name nomenclaturally (Article 12.3 of the Code of Zoological Nomenclature). Hence, the name *Crocodilus australis* as applied to the South American species must be attributed to Bravard in Burmeister (1885), making it a junior primary homonym of Crocodilus australis Krefft rather than the senior primary homonym that would be the case if Bravard had provided any diagnostic or descriptive details prior to his death.

The second use of *australis* with crocodiles is by Deraniyagala (1953) who, while describing Sri Lankan populations of the Saltwater Crocodile Crocodylus porosus, noted "The Australian form with its clusters of numerous raised post-occipital scutes might be termed Crocodylus porosus australis ssp. nov. (Vide Barrett 1950. Reptiles of Australia Cassell & Co., p. 12)." As noted by Mertens (1960), the plate in Barrett (1950) facing p. 12, while labelled as a Saltwater Crocodile, is of an American Alligator, Alligator mississippiensis, and clearly shows numerous raised postoccipital scutes, while there is no mention of this character, or of any other species-specific morphological character, on p. 12, and it is assumed that Deraniyagala's citation of p. 12 is a reference to the unnumbered plate facing this page. That Deraniyagala cited the incorrect page number does not invalidate the name nomenclaturally, as he stated the purported diagnostic character in his publication rather than merely making the name available by bibliographic reference to a diagnostic statement. Deraniyagala's name Crocodylus porosus australis has been placed in the synonymy of Alligator mississippiensis by Mertens (1960), and Wermuth & Mertens (1961), and it is hence unavailable for the Australian populations of Crocodylus porosus (although Wermuth & Mertens, 1977 and Cogger et al., 1983 retain it in the synonymy of Crocodylus porosus).

The third use of the name *australis* in crocodiles does, however, unequivocally relate to Australian populations of Crocodilus porosus and, like C. australis Krefft, appears to have been overlooked by all subsequent researchers. Gray (1867), while describing the Saltwater Crocodile (under the combination *Oophilus porosus*), noted that Australian populations differed from Indian populations in having "one cross band of the shield less than the Indian specimens; that is to say, they have sixteen, and the Indian specimens seventeen bands of shields from the neck to the base of the tail." Consequently, he used the name "var. australis" for Australian populations, though attributing the name to Alfred Günther, who had pointed out the difference to him. This stated diagnostic character is sufficient to validate the name Oophilus porosus var. australis for Australian populations of Crocodilus porosus, and antedates Deraniyagala's Crocodylus



Figure 1. Left lateral view of a dried head of *Crocodylus johnstoni*, possibly the holotype of *Crocodilus australis* Krefft and *Tomistoma krefftii* Gray, in Krefft (image created from Negative V343, Australian Museum Archives).

porosus australis by 86 years. The use of varietal status for the taxon qualifies as subspecific recognition (Article 45.6.4 of the Code of Zoological Nomenclature). Gray (1872) repeated the diagnostic statement. Both Gray (1867) and Krefft (1867) were published in the same year. Relative priority can be determined from the literature. Krefft's description, published on 27 July, antedates Gray's description, which was published on 5 November (Peavot, 1913).

Hence, in summary, Crocodilus australis Krefft, 1867 is a senior primary homonym of Crocodilus australis Bravard in Burmeister, 1885 (now Caiman australis), a senior secondary homonym in *Crocodylus* of *Oophilus porosus* var. *australis* Günther in Gray, 1867, but, by one letter difference in the generic name, not a homonym (but see Article 57.5 of the Code of Zoological Nomenclature for an alternative view, if Crocodilus is considered an incorrect subsequent spelling of Laurenti's Crocodylus) of Crocodylus porosus australis Deraniyagala, 1953, a synonym of Alligator mississippiensis, although intended by that author as a name for Australian populations of Crocodylus porosus, where it would have been a junior secondary homonym of Krefft's name as well as that of Günther in Gray (and a junior synonym of the latter). Whether Australian populations of saltwater crocodiles warrant subspecific recognition remains largely unstudied.

The type material of *Crocodilus australis* Krefft, 1867 and *Tomistoma krefftii* Gray, in Krefft, 1873

Krefft (1867), when describing Crocodilus Australis, refers to the specimen as a skull. However, the form of the same specimen when described as T. krefftii, is variably stated as either a skull or a head. Krefft (1873a) first states that he sent Gray a photograph of the skull, and notes that the skull was damaged during preparation (it is unclear whether this was Krefft's preparation of the skull, or prior preparation by the donor). On the same page, Gray's accompanying letter refers to the photograph sent to him as being of the "upper part of the head". On the next page, Krefft further states that the character state of the mandibular symphysis was apparent to him "only since the skin had been removed from the skull", suggesting that it was Krefft who removed the skin and prepared the skull, after sending a photograph of the head to Gray. However, it is possible that Krefft was actually saying that only he was able to examine the mandibular symphysis, since only he had the opportunity to examine the ventral surface of the skull, as Gray had been sent only a dorsal photograph.



Figure 2. Dorsal view of holotype skin of Crocodilus johnsonii Krefft.



Figure 3. Left lateral view of holotype skin of Crocodilus johnsonii Krefft.



Figure 4. Ventral view of holotype skin of *Crocodilus johnsonii* Krefft. Note the low number of transverse ventral scale rows on the body, diagnostic of this species.



Figure 5. Details of the point of removal of the head from the holotype skin of *Crocodilus johnsonii* Krefft. Right side, image reversed to allow comparison with Fig. 6, which is similarly reversed due to the method of illustration and printing.



Figure 6. Reproduction of image of the cast of the head of the holotype of *Crocodilus johnsonii* Krefft, from Gray (1874). Note correspondence of the posterior edge of the cast with the anterior edge of the holotype skin.

The combination of Krefft's (1873a) description of the damage to the specimen (damage by rats, with a broken rostrum and several missing teeth), and his earlier description of the skull being ten inches long, from an individual four or five feet long, should facilitate identification of this specimen among the skulls of *Crocodylus johnstoni* in the Australian Museum collection, if still present.

However, our search of the crocodile skulls among the early collections, and examination of registration records (the earliest Australian Museum collection registers postdate Krefft's era) has not revealed any suitable candidate specimen of the size and damage described, and we consider the skull that represents the holotype of both *Crocodilus australis* and *Tomistoma krefftii* to be lost. Indeed, there is no mention of this specimen in the monthly and annual Australian Museum donation lists for 1867, raising the possibility that it may have been retained by the collector after having been shown to Krefft and photographed by him.

The photograph of the type of *Tomistoma krefftii* sent by Krefft to Gray can now no longer be located in the Natural History Museum, London (P. Campbell, pers. comm.). While there is much Krefft correspondence in the Natural History Museum Archives, which the senior author has examined, no photographs are associated with the letters, and the crocodile correspondence cannot be located.

However, the Australian Museum Archives holds a glass plate negative (V343 in the Register of Negatives) of a lateral view of the dried head of a Crocodylus johnstoni (Fig. 1), depicted lying on a wooden bench with a 2 inch scale bar attached to the edge of the bench. Based on this scale bar. the head is approximately 10 inches long, and several teeth at the anterior end of the rostrum are missing. The Register of Negatives postdates Krefft's era, and the negatives are arranged in taxonomic order (reptile images are entered in the series V340-V361), and hence there is no useful information to be gathered from the order of registration on the date each negative was created. The negatives in the series are identified in the register as having been created by H. Barnes, presumably Henry Barnes Senior, who was taxidermist/ photographer during Krefft's curatorship, ending in 1874. Henry Barnes (4.iv.1838-17.iii.1898) was employed by the museum between 1859 and 1897; his son, Henry Edward Barnes (Henry Barnes Junior), was employed by the museum between 1878 and 1913 (Strahan, 1979). This cannot be the negative for the photograph sent to Gray by Krefft, as it shows a lateral view rather than a dorsal view, but it may be one of a series taken at the same time. If this photograph does represent the holotype of Crocodilus australis and the specimen of which the photograph was sent by Krefft to Gray on which the name Tomistoma krefftii was based, it must have been taken before the skin was removed and the rostrum damaged (broken and chewed by rats), as no such damage is apparent (at least on the left side of the head).

In the absence of extant type material, it becomes important to attempt to match any archival material available of the type specimen to a particular location or population from which the type was sourced, to stabilize the taxonomy and nomenclature of the species.

Where did William Wood collect in northern Queensland?

That Wood gave the specimen to Krefft shortly before Krefft described it as Crocodilus australis in July 1867 provides sufficient information to track Wood's source population. By July 1867, the only settled port in the Gulf of Carpentaria was Burke Town (also known in contemporary records as the Albert River Settlement, and now known as Burketown), which was established in 1865. The other coastal towns. Normanton and Karumba (initially known as Kimberley), were not established until 1867 in the case of the former and the 1870s for the latter. Examination of the published shipping records reveals the departure of a Mr W. Wood from Burke Town as one of two passengers (the other the local Police Lieutenant Wentworth D'Arcy Uhr, who was accompanying a prisoner) departing from Burketown aboard the schooner Salamander on 17 April 1867, and arriving in Sydney on 9 July, after a rough passage around the west coast of Australia and through Bass Strait (Anonymous, 1867a-c).

Hence, William Wood arrived in Sydney 18 days before the publication of the description of *Crocodilus australis*, and had been based in Burketown, which must be considered an approximate locality for the collection of the type. It is not clear how long Wood had lived in Burketown—we have been unable to find any record of his arrival in shipping records. He may have come to the district overland from Port Denison (now Bowen), along with many of the early settlers.

The type material of *Crocodilus johnsonii* Krefft, 1873

That Krefft (1873b) did not regard *Tomistoma krefftii* as conspecific with *C. johnsonii* at the time of description of the latter, clearly implies that the type of *T. krefftii* cannot be considered a part of the type series of *C. johnsonii*, although this is not obvious from the second description of the latter species (Krefft, 1873a) in the *ZSL Proceedings*.

Hence, the description of *Crocodilus johnsonii* by Krefft (1873b) must be based solely on the specimen collected by Mr Johnson [sic]. Krefft specifically states in both of his papers of that year that the specimen was the skin of a crocodile 7 feet in length, with the head 1 foot 4 inches. He further notes details of the head and neck in the description, which together with the total length given, indicates that the head was part of the skin at the time of the description.

Subsequently, the holotype of *Crocodilus johnsonii* has been considered to be represented by two specimens in the Australian Museum collection: a stuffed skin missing the head, registered in the Palmer Register as 4627, but now reregistered in the herpetology collection as AM R134547 (Figs 2–4), and an articulated skeleton, initially 4629 in the Palmer Register, but now AM R134548, considered to be from the same animal (Cogger, 1979; Cogger *et al.*, 1983; King, 1989; Shea & Sadlier, 1999). The Palmer Register has annotations for these two entries that appear to be in the hand of Allan McCulloch, employed by the Museum between 1901–1925. These state that the head was cast, and that the skeleton represented the same individual as the skin. This information is noted as being obtained from Edward Pierson Ramsay, who succeeded Krefft and died in 1916. Hence, these annotations are likely to have been made between 1901 and 1916, at least 27 years after Krefft's departure from the Museum, and at least 20 years after Krefft's death.

There is no record of when the head was removed from the rest of the skin, but the incisions on the remaining stuffed skin are certainly not fresh (Fig. 5). Gray had been sent a photograph approximately 22 inches long, showing a dorsal view of the whole specimen of the holotype of *C. johnsonii* (Gray, in Krefft, 1873a), while one year later Gray (1874) illustrated the head of the species, based on a plaster cast of the head of the holotype sent to him by Krefft.

The posterior margins of the illustration of the head (Fig. 6) provided by Gray (1874) correspond closely to the margins left on the remaining portion of the mount, and hence we presume that the head was removed by Krefft in 1873, shortly after the description of the species, to prepare the mould for the plaster cast and subsequently prepare the skull. The shape of the plaster cast illustration in Gray's (1874) paper indicates that the intact skull was still inside the head when it was cast. Preparation of the skull would have involved destruction of the skin of the head, which is firmly attached to the skull in crocodilians. The mould created for casting by Krefft could also provide a replacement head cast to complete the mounted skin for display following skull extraction, although this does not seem to have been done (possibly overlooked in the tumult following Krefft's dismissal as Curator in 1874-Pigott & Strahan, 1979). The mounted skin bears no evidence of glue or paint at the cut margins, although there is a little residual plaster along the ventral suture line, and there are no entries in the Australian Museum Register of Casts (the L Register) or Register of Moulds (the T Register) of a cast or mould of the whole head of either Palmer Register 4627 or 4629. The Register of Moulds, however, does include an entry relating to the mandible of Palmer Register 4629 (the skeleton), a mould registered as T71 (entered in September 1904, but copied from an older entry), and the Register of Casts has two entries for the mandible of Palmer Register 4629. The first, L71, bears no annotation that it was taken from the holotype mandible, but does bear a reference to the number 69, a number that also appears in association with the Mould Register entry for T71, but which we have not otherwise been able to trace. The second entry, L1462, registered on 27 July 1921, is specifically linked in the original entry to mould T71. This cast was recorded at the time of entry as part of the "Old Collection". It is not clear whether L71 from 1893 and L1462 from 1921 are the same cast, but neither has been further traced in the Australian Museum collection.

As the head and most of the dorsum of the neck are now missing from the mounted skin, precluding examination of many of the purported diagnostic features of the species relating to dentition, head shape and arrangement of nuchal plates, and as the purported holotype skin was not registered until several years after the description (the Palmer Register, the first register mentioning the specimen, was compiled between 1877 and 1880, and number 669, assigned to a mammal specimen, which appears well before the number assigned to the crocodile skin, has been interpreted as being assigned about 1879—Parnaby *et al.*, 2015), it is important to ensure that the skin actually does represent the holotype, and the species currently assigned the name *C. johnstoni*, rather than being a later substitute.

89

The major character states described from body, tail and limbs (the components still present on the skin) by Krefft (1873a,b) relate to the dorsal shields. Krefft describes those of the body as being one single row, one of two scales, two rows of four, two rows of six, seven rows of eight (the outer ones feebly keeled), two rows of six, and four rows of four, giving 19 rows to the base of the tail, with the tail in turn encircled by 29 bands of scales. All of these features are present on the extant portion of the mount. Given the correspondence of the cast of the head in the then British Museum collection (Gray, 1874; Boulenger, 1889) with the remaining mount in the Australian Museum, we consider that the remaining portion of the stuffed skin is assignable to the holotype specimen. While this specimen now lacks the cranial and nuchal features diagnostic of Crocodylus johnstoni (e.g., Cogger, 2014), it is identifiable as that species on the basis of the presence of osteoderms in the ventral body scales, and approximately 24 transverse rows of ventral body scales from the posterior nuchal collar to the anterior margin of the vent (Brazaitis, 1987).

The mounted skin is now black, possibly due to painting. There is some flaking of what appears to be thin paint on some dorsal scales. Consequently, the original pattern described by Krefft is no longer apparent.

The cast of the head of the holotype of *C. johnstoni* in the Natural History Museum, London, although mentioned as being present by Boulenger (1889) and King (1989) (the latter author may have simply based his statement on that of Boulenger), is no longer able to be located in the collection, and the herpetology catalogue lists it as unregistered (P. Campbell, pers. comm.). Hence, the only information that can be obtained from it is from the illustration of the cast provided by Gray (1874).

However, there are glass plate negatives in the Australian Museum Archives (V340–342, V344–345) that appear to represent the holotype stuffed skin. The first three of these negatives, which, like the other negatives in the series, are on standard 8×6 inch glass plates (c. 202×152 mm), represent a sequence of three segments of the specimen: head, torso and tail, with overlap between the images (Figs 7-9). Abutting these plates and exposing them directly onto photographic paper would have created an image about 22 inches long, assuming either some trimming of the blank space in front of the tip of snout and tip of tail, or overlapping of the plates in sequential exposures to eliminate redundancies (each image has what appears to be chalk marks between transverse rows of scutes on neck and tail that allow alignment of the images, although there are some perspective changes between images that prevent perfect alignment). V344 (Fig. 10) is a lateral view of the whole mount, placed on a timber table (but not the same table as the image of the possible type of C. australis), and V345 (Fig. 11) is a dorsal view of the whole animal, seemingly placed against the same white drape apparent on the wall in Fig. 10. All five negatives, which are identified in the Register of Negatives as Philas johnstonii (or possibly johnstonei-the handwriting could be interpreted either way), are clearly of the same specimen, and the torso and tail of the specimen correspond to the extant portions of



the holotype skin. The specimen represented is different to the head in image V343 (which we consider to represent the type of *Crocodilus australis* and *Tomistoma krefftii*).

These images, all identified as being taken by H. Barnes, would seem to be the basis of the 22 inch photograph sent to Grav in 1873, and would seem to represent the specimen prior to removal of the head for casting. However, there is one major discrepancy between the photographs and the cast. V344 shows the mouth of the mounted skin to be open, while the cast has a closed mouth. It is possible that Krefft forced the mouth closed prior to casting, to simplify the casting process. The position of the articulation between mandible and quadrate relative to the postarticular skin impression on the cast would have resulted in any tissue compression caused by closing of the mouth lying within the mouth (and hence not visible on the cast), while the relatively small amount of postarticular skin would be slightly stretched. Further, from comparison of the photograph of the head in dorsal view (Fig. 7) with Gray's 1874 figure (Fig. 6), it is apparent that Gray's figure is reversed, as might be expected from a print made from a lithographic etching that was not initially drawn in reverse (Gould, 1996; the reversal is most obvious in the asymmetry of the nuchal shields, but also apparent in more subtle asymmetries).

Krefft (1873a,b) makes no mention of a skeleton. The articulated skeleton that has subsequently been considered part of the type (Fig. 12) is currently missing the skull,

although this has evidently been removed from the mount at some time after preparation, as the steel rod passing through the vertebral canal to articulate the vertebral column extends 11 cm beyond the atlas to form a support for a skull.

There is currently only one isolated skull of *Crocodylus johnstoni* in the Australian Museum collection that lacks locality and collector data (R179146). From comparison of this skull with the illustration of the cast of the head of the holotype presented by Gray (1874), viewed in reverse, together with the observation by Krefft (1873a,b) that the head of the holotype was 1 foot 4 inches long (= 406 mm, although the reference points for this measurement were not provided), R179146 can be excluded from consideration as the missing holotype skull, as it has a midline skull length of 370 mm, a lateral skull length of 390 mm, and mandibular teeth 12–13 both interposed between teeth 12–13 of the upper dental arch.

Another possibility for the missing skull is that it is represented by the photograph provided by Waite (1929: 56) in his *Handbook of the Reptiles and Amphibians of South Australia*. Edgar Ravenswood Waite (5.v.1866–19.i.1928), prior to his appointment as curator of the South Australian Museum, was employed at the Australian Museum between 1893–1906, and hence would have had the opportunity to obtain photographs of the holotype. No *Crocodylus johnstoni* skull corresponding to this photograph can be located in the South Australian Museum collection (C. Kovach, pers.





93



Figure 12. Dorsal view of the mounted skeleton AM R134548, purported to be from the same individual as the holotype skin of *Crocodilus johnsonii* Krefft.



Figure 13. Dorsal view of vertebrae and ribs of AM R134548 at midbody, showing damage to the transverse processes and heads of ribs on right side, corresponding to the site of the presumed shot hole in the mounted skin.

comm.), and hence the photograph is likely to have come from a different collection, possibly the Australian Museum.

In the absence of the skull, is it possible to unequivocally link the postcranial skeleton to the skin, or if not, to the species? The general size and proportions of the postcranial skeleton match the skin, but there have been no detailed comparative anatomical studies of the postcranial osteology of the two Australian crocodile species that would allow certainty of identification. However, there is some forensic evidence that the skeleton and skin belong to the same specimen, additional to the information from Ramsay that was added to the original register entry by McCulloch. Johnstone (1904) reported that the holotype was shot by him. The holotype skin bears a repaired hole on the right side of the midline near midbody (Fig. 8) that presumably represents the damage made by the musket ball or rifle bullet. The skeleton has corresponding damage: the transverse processes on the right side of presacral vertebrae 15–18 and the heads of the corresponding ribs are missing, and have been replaced by sculpted artificial processes and rib heads (Fig. 13). The replacement transverse processes on the left side, and those bordering the repaired area on the right side.

Hence, we accept that the skeleton, although not mentioned in any of the early literature associated with the species, does derive from the same specimen as the skin, and should be treated as part of the holotype. Forensic DNA studies may provide further evidence to support this argument.

The type locality of Crocodilus johnsonii

As presented in both descriptions of the species (Krefft, 1873a,b), the holotype was collected by Robert Johns[t]on from Cardwell, Rockingham Bay. The registration entry in the Palmer Register merely gives the locality as the upper Herbert River. However, several subsequent listings (e.g., Wermuth, 1953; Mertens & Wermuth, 1955; Wermuth & Mertens, 1961, 1977; Cogger et al., 1983; King, 1998) give the type locality as Cashmere on the upper Herbert River. This emendation would appear to have been derived from a quotation from the collector included with a description of the cranial osteology by Longman (1925), which states that Johnston shot the specimen in the Herbert River, near the mounted police camp at Cashmere. This in turn was stated by Longman to have been derived from a newspaper clipping. Longman did not provide details of which newspaper the quote came from, but it seems to be an extract from Johnstone (1904). Cashmere (18°08'13"S 145°20'20"E) is approximately 74 km WNW of Cardwell, it is the given type locality and a more likely locality for the species than Cardwell. It correlates well with Johnstone's 1871 assignment to Cashmere to be the Acting Sub-Inspector at the mounted police camp there and also with his observations that he shot several specimens, after the first, in the same stretch of water. Cardwell, the originally given locality, is near the coast and below the Herbert River Falls, an area which Johnstone did not consider the species to inhabit.

The collector and donor of the holotype of *Crocodilus johnsonii*

Both descriptions of the species (Krefft, 1873a,b) give the collector as Mr Johnson, and note that the specimen was sent by Johnson to a Mr C. Blaxland, jun., of Ryde, for Krefft's examination (Krefft, 1873a, further spells the donor's name as Bloxland). However, in the list of donations to the Museum for November–December 1872, the donor's name is given as J. G. Blaxland (Krefft, 1873c), and that version is also given in a later "Letter to the Editor" by Krefft reporting a large python sent by Johnstone to Blaxland for Krefft (Krefft, 1873d). The donor is either John Gregory Blaxland (8.x.1801-26.i.1884) of The Hermitage, Ryde, son of the explorer Gregory Blaxland, and aged 71 at the time of donation, or his eldest son, also John Gregory Blaxland (17.x.1846–12.xii.1906), and 26 years of age. The Australian Museum Archives has a letter (C.30.73) from Blaxland to Krefft, dated 13 January 1873 (two weeks after Krefft wrote his manuscript for the Zoological Society of London), that explains some of the details of the transfer:

Ryde

13 Janry 1873

Dear Krefft

Your letter to me miscarried & I only received it last night—you addressed it to C. Blaxland J^r, whereas my name is John G. Blaxland. I am the donor of that specimen of the Crocodilus Johnsonii to the Museum—although I wished it named, as you have done, after the person who shot it—He is Sub Inspector of Police, at Cardwell—Rockingham Bay & his name is Robert Johnstone he takes great interest in natural history &c & if he collects any-thing rare will forward it to the Museum. He promised me this Crocodile a long time ago but when he sent it I thought I had better send it to you than try & preserve it myself—will you kindly have the card attached to it altered to "Presented by John G. Blaxland" & oblige

Yours truly

Jno. G. Blaxland."

Hence, while Krefft (1873a,b) initially gave the collector's name as Johnson, he was made aware of the error shortly after the newspaper account was published, and while the manuscript was en route to London. Krefft wrote to Gray on 15 May 1873 (while the description in the ZSL Proceedings was still awaiting printing), who published the correction early the following year (Gray, 1874), and Krefft himself, in his third article on Australian crocodiles (Krefft, 1874) also noted that the name was corrected to johnstonii "so as to indicate precisely the name of the discoverer". However, we, like Blaxland, note that the collector's name was Johnstone. He routinely spelt his name as Johnstone in his writings (e.g., Johnstone, 1904, and a number of other articles in the same series), and his biography in the Australian Dictionary of Biography is under the name Robert Arthur Johnstone (Jones, 1972).

What to do with the earlier names?

The existence of the earlier name Crocodilus australis Krefft, 1867 imperils the stability of nomenclature of Crocodylus johnstoni. Under the Code of Zoological Nomenclature, it is possible to reverse the priority of these two names, to maintain the usage of C. johnstoni to the species for which it has consistently been applied for almost 150 years (notwithstanding occasional use of the original spelling johnsoni-Tucker, 2010). Invoking Article 23.9, we note that Crocodilus australis has not been used as the available name for this species since it was first created by Krefft in 1867 (Article 23.9.1.1), while Crocodylus johnstoni has been used consistently as the available name for this species, including the following 25 papers and books published over the past 50 years, with more than 10 authors involved (Article 23.9.1.2): Britton et al. (2013), Campbell et al. (2010), Compton (1981), Firth et al. (2010), Grigg & Alchin (1976), Grigg & Kirschner (2015), Grigg et al. (2001), Hines & Skroblin (2010), Jamieson et al. (1997), Kennett & Christian (1993), Letnic & Ward (2005), Olsson & Phalen (2012), Renous et al. (2002), Richardson et al. (2002), Seebacher (1999), Smith & Phillips (2006), Somaweera et al. (2012), Taplin et al. (1982, 1999), Tucker et al. (2006), Walsh (1989), Webb & Manolis (1989), Webb et al. (1987), Whitehead & Seymour (1990), and Willis & Archer (1990). We further note that Grigg et al. (2001) is the edited proceedings of a conference, and contains 35 papers, of which 14, by a total of 27 authors, use the name Crocodylus johnstoni. Webb et al. (1987) is similarly an edited work based on a conference, containing 51 papers, of which 20, authored by various combinations of 20 authors, use Crocodylus johnstoni.

Hence, under Article 23.9, *Crocodilus australis* is a *nomen oblitum*, and cannot be used as the name for this species when both *C. australis* and *C. johnstoni* are considered conspecific.

However, it remains an available name, and should evidence arise that the populations to which the two names apply are not conspecific (or consubspecific), *C. australis* would become available for use for populations to the west of those represented by the type of *C. johnstoni* (Article 23.9.2, and associated Example).

Tomistoma krefftii, published simultaneously with C. johnsonii by Krefft (1873b), does not imperil stability of nomenclature, as it was placed in the synonymy of C. johnsonii by Krefft (1874), acting as First Revisor (Article 24.2). As it is a junior objective synonym of Crocodilus australis Krefft, it is permanently unavailable while C. australis remains available.

Krefft (1872, 1873b), in the two articles published in newspapers immediately after he wrote them (and hence unlikely to have been independently modified by scientific editors), and in the Museum's Annual Report for 1873 (Krefft, 1873e), used the -ii termination for the species epithet. This is contrary to the two papers that were published in the ZSL Proceedings (Krefft, 1873a; Krefft, in Gray, 1874), presumably without Krefft being able to see proofs of those papers, which used the single -i termination. This suggests that the -ii termination was his preference, and the -i orthography may have been an alteration to his manuscripts made by his London correspondents, particularly Gray. Under Article 33.4, and with recognition of the priority of the spelling by Krefft (1873b), the currently used -i form is to be considered an incorrect subsequent spelling, albeit one that, like the alteration of *johnsoni* to *johnstoni*, is now in general usage, and consequently, under Article 33.3.1, is to be maintained.

While the Code allows for reversal of priority of the name Crocodilus australis Krefft, 1867 and Crocodilus johnstoni without recourse to use of the Plenary Powers of the Commission, the same is not true for the primary and secondary homonymies created by the discovery of C. australis Krefft, due to the lack of use of the subsequent three australis epithets among crocodilians: Crocodilus australis Bravard, in Burmeister, 1885 has been rarely mentioned in the literature, although consistently recognized as a valid species of alligatorid when it is mentioned; Oophilus porosus var. australis Günther, in Gray, 1867 has been overlooked by all subsequent authors, and Crocodylus porosus australis Deraniyagala, 1953 has remained in synonymy (of either C. porosus or Alligator mississippiensis) since 1960, and hence none fulfill Article 23.9.1.2. In order to maintain usage of Crocodilus australis Bravard, in Burmeister, and to remove the secondary homonymy with *Oophilus porosus* var. australis Günther, in Gray within Crocodylus, a request to the ICZN should be prepared to suppress C. australis Krefft for the purposes of homonymy, or a replacement name be provided for the fossil caiman. We leave this to specialists in South American alligatorid palaeontology to decide.

We summarise the findings of our paper with the following synonymy for *Crocodylus johnstoni*:

Crocodylus johnstoni Krefft, 1873

- *Crocodilus australis* Krefft, 1867, *The Australasian* (new series) 3(69): 8 (*nomen oblitum* with respect to *Crocodilus johnstoni*, action taken here under Article 23.9 of the Code of Zoological Nomenclature).
 - Holotype: a skull donated to the Australian Museum, lost, collected by William Wood.
 - Type locality: Gulf of Carpentaria (actual place of capture, the hinterland of Burketown, based on collector's known movements).
 - Not Oophilus porosus var. australis Günther, in Gray, 1867, Transactions of the Zoological Society of London 6: 138 (now in synonymy of Crocodylus porosus); not Crocodilus australis Bravard, in Burmeister, 1885, Anales del Museo Nacional de Buenos Aires 3(2): 148 (now Caiman australis); not Crocodylus porosus australis Deraniyagala, 1953, A Colored Atlas of Some Vertebrates from Ceylon, volume 2: 34 (now in synonymy of Alligator mississippiensis).
- Crocodilus johnsonii Krefft, 1873, Sydney Mail and New South Wales Advertiser (new series) 15(653): 8.
 - Holotype: AM R134547, mounted skin, missing head; AM R134568, skeleton missing skull, Upper Herbert River, collected by R. Johnson [Johnstone], donated J. G. Blaxland.
 - Type locality: Cardwell, Rockingham Bay (corrected to Cashmere, upper Herbert River, by the collector—Johnstone, 1904).
- Tomistoma krefftii Gray, in Krefft, 1873, Sydney Mail and New South Wales Advertiser (new series) 15(653):
 8 (junior objective synonym of Crocodilus australis Krefft; synonymy with Crocodilus johnsonii by Krefft, 1874).

Holotype: as for Crocodilus australis Krefft.

Type locality: as for Crocodilus australis Krefft.

- Crocodilus johnsoni Krefft, 1873, Proceedings of the Zoological Society of London 1873: 334 (incorrect subsequent spelling of Crocodilus johnsonii Krefft, 1873, Sydney Mail and New South Wales Advertiser [new series] 15[653]: 8).
- Crocodilus johnstoni Krefft, in Gray, 1874, Proceedings of the Zoological Society of London 1874: 177 (emendation of Crocodilus johnsoni Krefft, 1873, Proceedings of the Zoological Society of London 1873: 334, preserved under Article 33.3.1 of the Code of Zoological Nomenclature).
- Crocodilus johnstonii Krefft, 1874, Sydney Mail and New South Wales Advertiser 18(750): 630 (emendation of Crocodilus johnsonii Krefft, 1873, Sydney Mail and New South Wales Advertiser [new series] 15[653]: 8).

ACKNOWLEDGMENTS. We thank Patrick Campbell (Natural History Museum, London) for attempting to locate the Krefft photographs and cast in that collection on our behalf, Jon Shepherd, Daisy Cunynghame and other staff at the Archives of that institution for their assistance to the senior author in examining the Krefft correspondence during visits in 2013 and 2014, Colin Johnston (Australian Museum production team) for access to a skull on display at the museum, Carolyn Kovach (South Australian Museum) for searching that collection for any potential source of the skull illustrated by Waite, and Rose Docker and especially Elizabeth McKinnon (Australian Museum Archives) for locating the negatives of the images of the type specimens and providing high resolution scans, and for tracking down Blaxland's letter. Hal Cogger and Harry Parnaby provided valuable comments on the manuscript.

References

- Albert, J. S., and R. E. Reis. 2011. Historical biogeography of Neotropical freshwater fishes. *Ameghiniana* 44: 427–434. http://dx.doi.org/10.1525/california/9780520268685.001.0001
- Ambrosetti, J. B. 1887. Observaciones sobre los reptiles fósiles oligocenos de los terrenos terciarios antiguos del Paraná. *Boletin de la Academia Nacional de Ciencias en Córdoba* 10: 409–426.
- Anonymous. 1867a. The Gulf Country. *Brisbane Courier* 22(3042) 11 July 1867: 3.
- Anonymous. 1867b. Ships' Mails. Empire (4890) 10 July 1867: 4.
- Anonymous. 1867c. Shipping. Arrivals.—July 9. Sydney Morning Herald 56(9088) 10 July 1867: 4.
- Barrett, C. 1950. Reptiles of Australia. Crocodiles, Snakes and Lizards. London: Cassell & Company, pp. 168.
- Bona, P., D. Riff, and Z. Brandoni de Gasparini. 2013. Late Miocene crocodylians from northeast Argentina: new approaches about the austral components of the Neogene South American crocodilian fauna. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103: 551–570. http://dx.doi.org/10.1017/S175569101300042X
- Boulenger, G. A. 1889. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History). London: Trustees of the British Museum, pp. x+311, pl. vi.
- Bravard, A. 1858. Monografia de los terrenos marinos terciarios, de las cercanías del Paraná. Argentina: Imprenta del Registro Official, pp. 107. [Not seen—citation based on Bravard, 1883, Bona et al., 2013, and Albert & Reis, 2011].
- Bravard, A. 1860. Catalogue des espèces d'animaux fissiles recueillies dans l'Amerique du Sud de 1852–1860. Paris: Privately printed. [Not seen—citation based on Bona et al., 2013]
- Bravard, A. 1883. Monografía de los terrenos marinos terciarios, de las cercanías del Paraná [reprint]. Anales del Museo Público de Buenos Aires 3(1): 45–94. [Note: journal title based on issue 1—volume title changed by the completion of the volume in 1891 to Anales del Museo Nacional de Buenos Aires].
- Brazaitis, P. 1987. Identification of crocodilian skin and products.
 In *Wildlife Management: Crocodiles and Alligators*, ed. G. J.
 W. Webb, S. C. Manolis, and P. J. Whitehead, pp. 373–386.
 Chipping Norton, New South Wales: Surrey Beatty & Sons.
- Britton, A. R. C., E. K. Britton, and C. R. McMahon. 2013. Impact of a toxic invasive species on freshwater crocodile (*Crocodylus johnstoni*) populations in upstream escarpments. Wildlife Research 40: 312–317.

http://dx.doi.org/10.1071/WR12215

Burmeister, G. 1885. Exámen critic de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precendente. *Anales del Museo Nacional de Buenos Aires* 3(2): 95–174 + pl. II–III. Campbell, H. A., S. Sullivan, M. A. Read, M. A. Gordos, and C. E. Franklin. 2010. Ecological and physiological determinants of dive duration in the freshwater crocodile. *Functional Ecology* 24: 103–111.

http://dx.doi.org/10.1111/j.1365-2435.2009.01599.x

- Cogger, H. G. 1979. Type specimens of reptiles and amphibians in the Australian Museum. *Records of the Australian Museum* 32(4): 163–210. http://dx.doi.org/10.3853/j.0067-1975.32.1979.455
- Cogger, H. G. 2014. *Reptiles and Amphibians of Australia*. Seventh Edition. Collingwood, Victoria: CSIRO Publishing, pp. xxx+1033.
- Cogger, H. G., E. E. Cameron, and H. M. Cogger. 1983. Zoological Catalogue of Australia. Volume 1. Amphibia and Reptilia. Canberra: Australian Government Publishing Service, pp. vi+313.
- Compton, A. 1981. Courtship and nesting behaviour of the freshwater crocodile, *Crocodylus johnstoni*, under controlled conditions. *Australian Wildlife Research* 8: 445–450. http://dx.doi.org/10.1071/WR9810443
- Cope, E. D. 1900. The crocodilians, lizards, and snakes of North America. In *Report of the U.S. National Museum, under the direction of the Smithsonian Institution, for the year ending June 30, 1898*, pp. 155–1270 + pl. 1–36.
- Deraniyagala, P. E. P. 1953. A Colored Atlas of Some Vertebrates from Ceylon. Volume 2. Tetrapod Reptilia. Colombo: Ceylon Government Press, pp. 101, pl. xi+35.
- de Saez, M. D. 1928. Sobre un yacaré de la formación Paranense. Anales de la Sociedad Científica Argentina 106: 67–72.
- Duncan, F. M. 1937. On the dates of publication of the Society's "Proceedings," 1859–26. Proceedings of the Zoological Society of London A107: 71–84. http://dx.doi.org/10.1111/j.1469-7998.1937.tb08500.x
- Firth, B. T., K. A. Christian, I. Belan, and D. J. Kennaway. 2010. Melatonin rhythms in the Australian freshwater crocodile (*Crocodylus johnstoni*): a reptile lacking a pineal complex? Journal of Comparative Physiology B. Biochemical, Systematic, and Environmental Physiology 180: 67–72.

http://dx.doi.org/10.1007/s00360-009-0387-8

- Gould, S. J. 1996. Left snails and right minds. In *Dinosaur in a Haystack*, pp. 202–217. London: Penguin Books.
- Gray, J. E. 1867. Synopsis of the species of recent Crocodilians or Emydosaurians, chiefly founded on the specimens in the British Museum and the Royal College of Surgeons. *Transactions of the Zoological Society of London* 6: 125–169 + pl. xxxi–xxxiv. http://dx.doi.org/10.1111/j.1096-3642.1867.tb00575.x
- Gray, J. E. 1872. Catalogue of Shield Reptiles in the Collection of the British Museum. Part II. Emydosaurians, Rhynchocephalia, and Amphisbaenians. London: Trustees of the British Museum, pp. vi+41.
- Gray, J. E. 1874. On *Crocodilus johnstoni*. *Proceedings of the Zoological Society of London* 1874(I): 177–178. http://dx.doi.org/10.1111/j.1096-3642.1874.tb02469.x
- Grigg, G. C., and J. Alchin. 1976. The role of the cardiovascular system in thermoregulation of *Crocodylus johnstoni*. *Physiological Zoology* 49: 24–36. http://dx.doi.org/10.1086/physzool.49.1.30155674
- Grigg, G. [C.], and D. Kirschner. 2015. Biology and Evolution of Crocodylians. Clayton South, Victoria: CSIRO Publishing, pp. xviii+649.
- Grigg, G. C., F. Seebacher, and C. E. Franklin. 2001. Crocodilian Biology and Evolution. Chipping Norton, New South Wales: Surrey Beatty & Sons, pp. x+446.
- Hines, K. N., and A. Skroblin. 2010. Australian freshwater crocodile (Crocodylus johnstoni) attacks on humans. Herpetological Review 41: 430–433.

- Jamieson, B. G. M., D. M. Scheltinga, and A. D. Tucker. 1997. The ultrastructure of spermatozoa of the Australian freshwater crocodile, *Crocodylus johnstoni* Krefft, 1873 (Crocodylidae, Reptilia). *Journal of Submicroscopic Cytology and Pathology* 29: 265–274.
- Johnstone, R. A. 1904. Spinifex and Wattle. Reminiscences of Pioneering in Northern Queensland. *The Queenslander* (1997) 18 June 1904: 27.
- Jones, D. 1972. Johnstone, Robert Arthur (1843–1905). In Australian Dictionary of Biography, volume 4: 1851–1890. D-J, ed. B. Nairn, G. Serle and R. Ward, pp. 486–487. Carlton, Victoria: Melbourne University Press.
- Kälin, J. A. 1936. Hispanochampsa mülleri nov. gen. nov. sp., ein neuer Crocodilide aus dem uneren Oligocaen von Tarrega (Catalonien). Abhandlungen der Schweizerischen Paläontologischen Gesellschaft 58: 1–40 + pl. I–II.
- Kennett, R., and K. Christian. 1993. Aestivation by freshwater crocodiles (Crocodylus johnstoni) occupying a seasonally ephemeral creek in tropical Australia. In Herpetology in Australia: A Diverse Discipline, ed. D. Lunney and D. Ayers, pp. 315–319. Sydney: Royal Zoological Society of New South Wales and Surrey Beatty & Sons.
- King, F. W. 1989. Order: Crocodylia. In Crocodilian, Tuatara, and Turtle Species of the World. A Taxonomic and Geographic Reference, ed. F. W. King and R. L. Burke, pp. 315–319. Washington, D.C.: Association of Systematics Collections.
- Krefft, G. 1867. Australian Crocodiles. *The Australasian* (new series) 3(69) 27 July 1867: 8.
- Krefft, G. 1871. The Natural History of New South Wales. Sydney Mail and New South Wales Advertiser (new series) 12(557) 4 March 1871: 22.
- K[refft], G. 1872. List of donations to the Australian Museum during March 1872. Sydney Morning Herald 65(10575) 10 April 1872: 3.
- Krefft, G. 1873a. Remarks on Australian Crocodiles, and Description of a New Species. *Proceedings of the Zoological Society of London* 1873(II): 334–335.
- Krefft, G. 1873b. Natural History. Remarks on Australian Crocodiles. Sydney Mail and New South Wales Advertiser (new series) 15(653) 4 January 1873: 8.
- [Krefft, G.] 1873c. List of donations to the Australian Museum during November and December, 1872. *Sydney Morning Herald* 67(10854) 1 March 1873: 8.
- Krefft, G. 1873d. Something like a snake. Sydney Morning Herald 68(11041) 6 October 1873: 13.
- Krefft, G. 1873e. List of donations to the Australian Museum during the year 1872. In Australian Museum. (Report from Trustees, for 1872), pp. 3–5. Sydney: Thomas Richards, Government Printer.
- Krefft, G. 1874. The Reptiles of Australia. Recent and Fossil. Sydney Mail and New South Wales Advertiser 18(750) 14 November 1874: 630.
- Langston, W. 1965. Fossil crocodilians from Columbia and the Cenozoic history of the Crocodilia in South America. University of California Publications in Geological Sciences 52: 1–152.
- Laurenti, J. N. 1768. Specimen Medicum, exhibens Synopsin Reptilium emendatum cum experimentis circa venena et antidota reptilium austriacorum. Viennae: Joan[nis] Thom[ae] Nob. de Trattnern, pp. 214 + Tab. I–V. http://dx.doi.org/10.5962/bhl.tttle.5108
- Letnic, M., and S. Ward. 2005. Observations of freshwater crocodiles (Crocodylus johnstoni) preying upon cane toads (Bufo marinus) in the Northern Territory. Herpetofauna 35: 98–100.
- Longman, H. A. 1925. Crocodilus johnsoni Krefft. Memoirs of the Queensland Museum 8: 95–102.
- Mertens, R. 1960. Zur Systematik und Nomenklatur der Ceylon-Krokodile. Senckenbergiana Biologica 41: 267–272.

Mertens, R., and H. Wermuth. 1955. Die rezenten Schildkröten, Krokodile und Brückenechsen. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 83: 323–440.

97

- Olsson, A., and D. Phalen. 2012. Preliminary studies of chemical immobilization of captive juvenile estuarine (*Crocodylus porosus*) and Australian freshwater (*C. johnstoni*) crocodiles with medetomidine and reversal with atipamezole. *Veterinary Anaesthesia and Analgesia* 39: 345–356. http://dx.doi.org/10.1111/j.1467-2995.2012.00721.x
- Parnaby, H., S. Ingleby, and A. Divljan. 2015. Taxonomic status of *Podabrus albocaudatus* Krefft, 1872 and declaration of *Sminthopsis granulipes* Troughton, 1932 (Marsupialia: Dasyuridae) as a protected name for the White-tailed Dunnart from Western Australia. *Zootaxa* 3904: 283–292. http://dx.doi.org/10.11646/zootaxa.3904.2.7
- Patterson, G. 1936. *Caiman latirostris* from the Pleistocene of Argentina, and a summary of South American Cenozoic Crocodilia. *Herpetologica* 1: 43–54, 1 pl.
- [Peavot, H.] 1913. List of dates of publication of the early parts of the Society's "Transactions". *Proceedings of the Zoological Society of London* 1913(III): 814–815.
- Pigott, A., and R. Strahan. 1979. Trustee-ridden 1860–1874. In Rare and Curious Specimens. An Illustrated History of the Australian Museum 1827–1879, ed. R. Strahan, pp. 27–35. Sydney: Australian Museum.
- Renous, S., J.-P. Gasc, V. L. Bels, and R. Wicker. 2002. Asymmetrical gaits of juvenile *Crocodylus johnstoni*, galloping Australian crocodiles. *Journal of Zoology* 256: 311–325. http://dx.doi.org/10.1017/S0952836902000353
- Richardson, K. C., G. J. W. Webb, and S. C. Manolis. 2002. *Crocodiles Inside Out.* Chipping Norton, New South Wales: Surrey Beatty & Sons, pp. 172.
- Rovereto, G. 1912. Los cocodrilos fósiles de las capas del Paraná. Anales del Museo Nacional de Historia Natural de Buenos Aires 22: 339–369 + pl. xvi–xviii.
- Schneider, J. G. 1801. Historiae Amphibiorum naturalis et literariae. Fasciculus Secundus continens Crocodilos, Scincos, Chamaesauras, Boas, Pseudoboas, Elapes, Angues, Amphisbaenas et Caecilias. Jena, Germany: Fried[rich] Frommann, pp. vi+364.
- Seebacher, F. 1999. Behavioural postures and the rate of body temperature change in wild freshwater crocodiles, *Crocodylus johnstoni*. *Physiological and Biochemical Zoology* 72: 57–63. http://dx.doi.org/10.1086/316638
- Shea, G. M., and R. A. Sadlier. 1999. A catalogue of the non-fossil amphibian and reptile type specimens in the collection of the Australian Museum: types currently, previously and purportedly present. *Technical Reports of the Australian Museum* 15: 1–91. http://dx.doi.org/10.3853/j.1031-8062.15.1999.1290
- Smith, J. G., and B. L. Phillips. 2006. Toxic tucker: the potential impact of cane toads on Australian reptiles. *Pacific Conservation Biology* 12: 40–49.

http://dx.doi.org/10.1071/PC060040

Somaweera, R., R. Shine, J. Webb, T. Dempster, and M. Letnic. 2012. Why does vulnerability to toxic invasive cane toads vary among populations of Australian freshwater crocodiles? *Animal Conservation* 16: 86–96.

http://dx.doi.org/10.1111/j.1469-1795.2012.00578.x

- Taplin, L. E., G. C. Grigg, P. Harlow, T. M. Ellis, and W. A. Dunson. 1982. Lingual salt glands in *Crocodylus acutus* and *C. johnstoni* and their absence from *Alligator mississippiensis* and *Caiman crocodilus. Journal of Comparative Physiology* 149: 43–47. http://dx.doi.org/10.1007/BF00735713
- Tucker, A. D. 2010. The correct name to be applied to the Australian freshwater crocodile, *Crocodylus johnstoni* [Krefft 1873]. *Australian Zoologist* 35: 432–434. http://dx.doi.org/10.7882/AZ.2010.029

- Tucker, A. D., C. J. Limpus, K. R. McDonald, and H. I. McCallum. 2006. Growth dynamics of freshwater crocodiles (*Crocodylus johnstoni*) in the Lynd River, Queensland. Australian Journal of Zoology 54: 409–415. http://dx.doi.org/10.1071/Z006099
- Waite, E. R. 1929. *The Reptiles and Amphibians of South Australia*. Adelaide: Harrison Weir, Government Printer, pp. 270.

Walsh, B. 1989. Aestivation in the Australian freshwater crocodile? Australian Zoologist 25: 68–70.

- http://dx.doi.org/10.7882/AZ.1989.004
- Webb, G. [J. W.], and [S.] C. Manolis. 1989. *Crocodiles of Australia*. Frenchs Forest, New South Wales: Reed Books, pp. 160.
- Webb, G. J. W., S. C. Manolis, and P. J. Whitehead. 1987. Wildlife Management: Crocodiles and Alligators. Chipping Norton, New South Wales: Surrey Beatty & Sons, pp. xiv+552.
- Wermuth, H. 1953. Systematik der rezenten Krokodile. *Mitteilungen aus dem Zoologischen Museum in Berlin* 29: 375–514. http://dx.doi.org/10.1002/mmnz.19530290203

- Wermuth, H., and R. Mertens. 1961. Schildkröten Krokodile Brückenechsen. Jena, Germany: Gustav Fischer, pp. xxvi+422.
- Wermuth, H., and R. Mertens. 1977. Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia. *Das Tierreich* 100: i–xxvii + 1–174.
- Whitehead, P. J., G. J. W. Webb, and R. S. Seymour. 1990. Effect of incubation temperature on development of *Crocodylus johnstoni* embryos. *Physiological Zoology* 63: 949–964. http://dx.doi.org/10.1086/physzool.63.5.30152623
- Willis, P. M. A., and M. A. Archer. 1990. A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. *Memoirs of the Queensland Museum* 28: 159–163.

Manuscript submitted 4 February 2016, revised 24 August 2016, and accepted 25 August 2016.