Dwarfism and feeding behaviours in Oligo-Miocene crocodiles from Riversleigh, northwestern Queensland, Australia

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Instances of dwarfism in the fossil record are of interest to palaeontologists because they often provide insight into aspects of palaeoecology. Fossil species of Australian-Pacific mekosuchine genus *Mekosuchus* have been described as dwarf, primarily terrestrial crocodiles, in contrast with the nearly ubiquitous semi-aquatic habitus of extant crocodilians (Willis 1997). This hypothesis has been difficult to test because of limited knowledge of the cranial and postcranial skeleton of extinct taxa and the continuous nature of crocodilian growth. New crocodilian vertebral material from Riversleigh, northwestern Queensland, tentatively referred to *Mekosuchus whitehunterensis*, displays morphological maturity indicative of adult snout-vent length little over a half-meter, proportionally smaller than extant dwarf taxa. Further, this material displays morphology that indicates a relatively large epaxial neck musculature for its body-size. These attributes suggest this dwarf mekosuchine employed unusual feeding behaviours. The ability to perform normal death-roll, de-fleshing behaviours would be limited in a mekosuchine of such small size. Given the powerful neck muscles and other anatomical features, it is more likely that this mekosuchine killed and/or dismembered its prey using a relatively forceful lifting and shaking of the head.

Key words: Crocodilia, Mekosuchinae, dwarfism, neural central suture, epaxial musculature, Oligo-Miocene, Australia, Riversleigh.

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Introduction

Difference in body-size between sympatric congeners is a key feature of trophic guilds and by extension ecosystems (Cohen et al. 1993; Hanken and Wake 1993; Brown et al. 2004; Woodward et al. 2005; Naisbit et al. 2012). Australian-Pacific species of *Mekosuchus* and *Trilophosuchus* have been suspected of being dwarf mekosuchine crocodiles (Willis 1993, 1997). Dwarfism in crocodilians is a function of growth rate. Growth in crocodilians is constant through life, but annual growth rates decrease towards maturity (Erickson and Brochu 1999). The timing of this event determines the average snout-vent length of a species. Dwarf forms result from comparatively early onset of decreased growth rates. Distinguishing dwarf adults from juveniles of larger sized crocodilian taxa can be difficult if growth series are not available (Dodson 1975; Webb and Manolis 1989) and such is the case for most mekosuchines (Willis 1993, 1997).

Size-independent identification of mature crocodilians in the fossil record was discussed by Brochu (1996). The present paper elaborates on this approach, focusing on new vertebral material of the apparently dwarf mekosuchine *Mekosuchus whitehunterensis* Willis, 1997, the earliest known species of the genus, from Oligo-Miocene deposits in the Riversleigh World Heritage Area, northwestern Queensland. Its vertebrae also provide new information about the hypothesized terrestrial behaviour of this species (Willis 1997).

Institutional abbreviations.—AR, research vertebrate paleontological collections (Archer collections), University of New South Wales, Sydney, Australia; QM F, palaeontological collections, Queensland Museum, Brisbane, Australia.

Other abbreviations.—CHant, anterior dorsoventral height of centrum; CHpost, posterior dorsoventral height of centrum; CL, anteroposterior length of centrum; CWant, an-

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terior mediolateral width of centrum; CWpost, posterior mediolateral width of centrum; NAH, dorsoventral height of neural arch; NCS, neurocentral suture; SA, surface area; ZL, anteroposterior length of zygapophyses; ZWant, mediolateral width of anterior zygapophyses; ZWpost, mediolateral width of posterior zygapophyses.

Material and methods

Five cervical vertebrae with associated remains of a left maxilla and left dentary were collected from Price is Right Site at Riversleigh. Additional vertebrae, one cervical and one thoracic, were collected from Riversleigh's Hiatus Site, and a single cervical vertebrae was collected from Riversleigh's LSO Site. The local faunas from LSO and Hiatus Sites are recognised as part of Riversleigh's Faunal Zone A and as such interpreted to be late Oligocene in age, while the Price is Right local fauna represents Faunal Zone B and as such regarded to be early Miocene in age (Travouillon et al. 2006, 2011). Anatomical terms used here follow Brochu (1996).

Measurements were taken to within the nearest 0.1 mm and mm^2 using Vernier callipers and the ImageJ software package (Tables 1, 2). Ontogenetic age was determined using the criteria described by Brochu (1996) based on the condition of the neurocentral suture (NCS) between the vertebral centrum and the vertebral neural arch. The NCS of each vertebra was classified as one of three states defined by Brochu (1996). The open state refers to the NCS being visible along the entire length of both sides of the vertebra, partial closure indicates the NCS is visible in part along either side of the vertebra, and in full closure the NCS is not visible.

Systematic palaeontology

Order Crocodylia Gmelin, 1788

Family Crocodylidae Cuvier, 1807

Subfamily Mekosuchinae Willis, Molnar, and Scanlon, 1993

Genus *Mekosuchus* Balouet and Buffetaut, 1987

Type species: *Mekosuchus inexpectatus* Balouet and Buffetaut, 1987, New Caledonia, Holocene.

?*Mekosuchus whitehunterensis* Willis, 1997

Figs. 1, 2.

Holotype: QM F31051, right maxilla.

Type locality: White Hunter Site, Riversleigh World Heritage Area, northwestern Queensland, Australia.

Type horizon: Riversleigh Faunal Zone A, late Oligocene.

Material.—Specimens from Price is Right Site: QM F56039, axis vertebra; QM F56040, third cervical vertebra; QM F56041, fourth cervical vertebra; QM F56042, sixth cervical vertebra; QM F56043, ninth cervical vertebra; QM F56046, left maxilla associated with QM F56039–43; QM F56047, left dentary associated with QM F56046 and QM F56039–43; from Hiatus Site: QM F56320, third cervical vertebra; QM F56321, third thoracic vertebra; from LSO Site: QM F56322, eighth cervical vertebra.

Description.—*QM F56046*: Left maxilla (Fig. 1A). Five alveoli and three teeth are preserved. Alveoli are circular in shape and form convex anterior and posterior dentigerous margins offset from a vaulted palate. The anterior-most tooth is enlarged. The remaining teeth are small and rounded. The height of the maxillary wall indicates that the rostrum was relatively deep. The medial surface is heavily sculptured.

QM F56047: Left dentary (Fig. 1B). Ten alveoli and three teeth are preserved. The teeth are small and rounded. The alveoli are all small, equally sized, and circular. The three anterior-most alveoli display a more buccal position than those following. The dentary deepens posteriorly. The preserved medial surface displays sculptural pits similar to those present in the maxilla QM F56046.

QM F56039: Axis vertebra (Fig. 2A). The odontoid process is not preserved. The spinous process is dorsoventrally tall and situated anteriorly on the neural arch. This process and the zygapophyses form an angle of approximately 20° with respect to the long axis of the centrum in lateral view. The NCS displays the open state.

QM F56040: Partial third cervical vertebra (Fig. 2B). The tall and narrow spinous process extends dorsally, perpendicular to the neural arch. Much of the centrum is missing. The NCS is partially open but to a lesser extent than occurs in the axis vertebra QM F56039. Partial closure is evident at the anterior and posterior-most ends of the NCS on both right and left sides.

QM F56041: Fourth cervical vertebra (Fig. 2C). The preserved base of the spinous process extends dorsal to the neural arch, as in the third cervical vertebra QM F56040. The hypapophysis is rounded and inclines weakly anteroventrally. The NCS displays an advanced state of partial closure, with a small open portion visible only on the left side.

QM F56042: Sixth cervical vertebra (Fig. 2D). The spinous process is missing and the hypapophysis is fractured. The NCS displays the closed state. There is considerable fracturing of the centrum on both right and left sides but this is distinct from the line of the NCS.

QM F56043: Ninth cervical vertebra (Fig. 2E). The preserved base of the spinous process indicates that it inclined weakly posteriodorsally. The hypapophysis is elongate and inclines more steeply anterioventrally than in the fourth cervical vertebra QM F56041. The NCS displays the closed state.

QM F56320: Third cervical vertebra (Fig. 2G). The left portion of the neural arch and the spinous process are missing. The hypapophysis is moderately elongate, narrowing distally, but inclines steeply anterioventrally. The NCS displays an effectively closed state, with only a faint imprint visible on the right side.

QM F56321: Third thoracic vertebra (Fig. 2F). The spi-

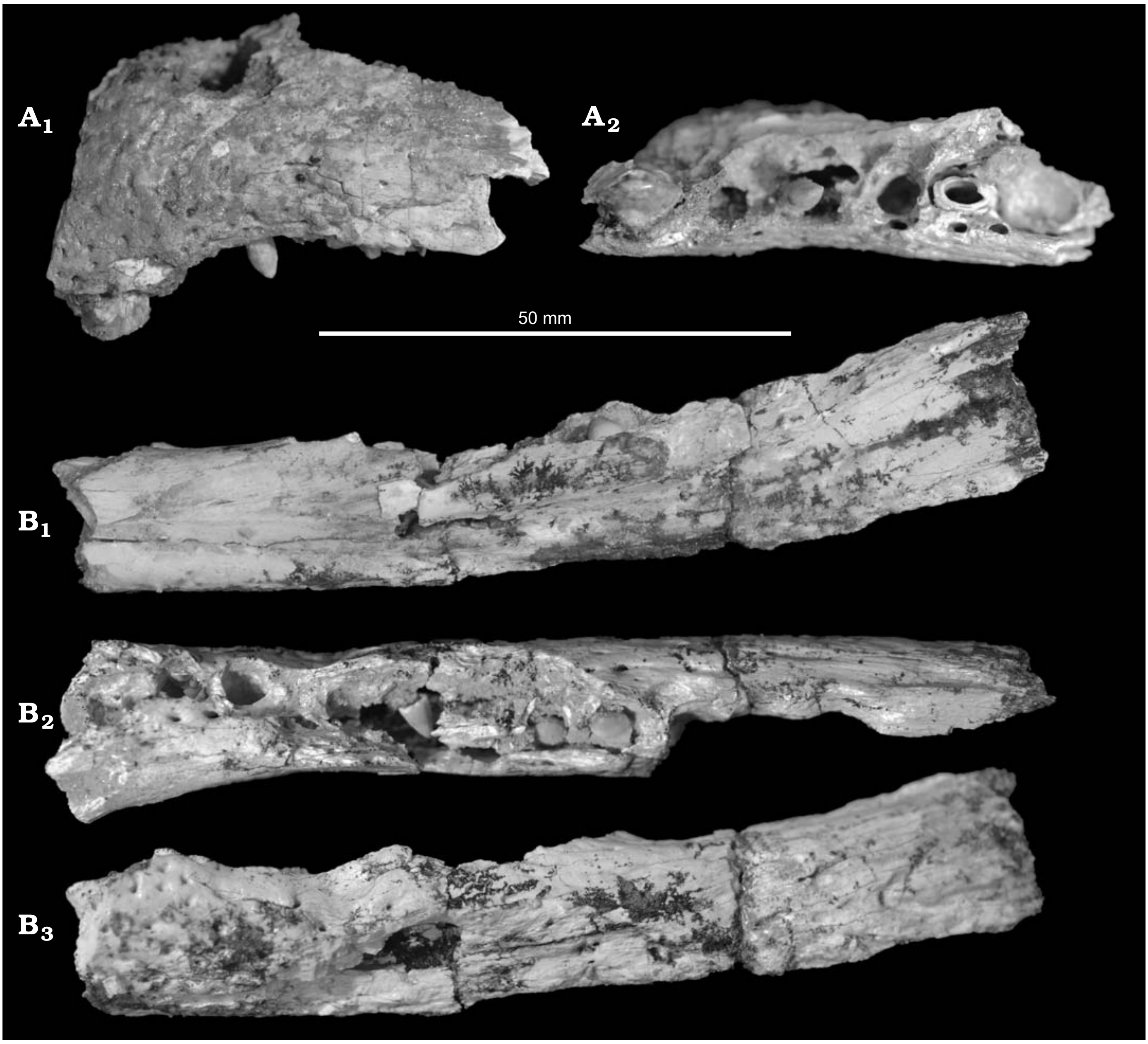

Fig. 1. Rostra of mekosuchine crocodile *Mekosuchus whitehunterensis* Willis, 1997; White Hunter Site, Riversleigh World Heritage Area, northwestern Queensland, Australia; late Oligocene. **A**. Left maxilla (QM F56046) in buccal (A_1) and ventral (A_2) views. **B**. Left dentary (QM F 56047) in lingual (B_1), dorsal (B_2), and buccal (B_3) views.

nous process is missing. The hypapophysis is reduced in size compared to those in the cervical vertebrae but inclines anterioventrally to a similar degree as the ninth cervical vertebra QM F56043. The NCS displays the closed state. Two small pits are visible ventral to the NCS on the right side, but these appear to be the result of post-mortem pitting of the surface unrelated to the NCS.

QM F56322: Eighth cervical vertebra (Fig. 2H). The spinous process is relatively tall and narrow, similar to the spinous process in the third cervical vertebra QM F56040, but inclines weakly posteriodorsally as in the ninth cervical vertebra QM F56043. The hypapophysis is elongate and inclines weakly anterioventrally, to a similar degree again as QM F56043. The NCS is in an advanced state of partial closure. Unfused portions of the NCS do not form contiguous lines. The left side of the NCS is about half as well fused as it is on the right side.

Geographical and stratigraphical range.—Northwestern Queensland, Australia, late Oligocene to early Miocene.

Discussion

The rostral materials, QM F56046 and QM F56047, appear to be referable to *Mekosuchus whitehunterensis* as diag-

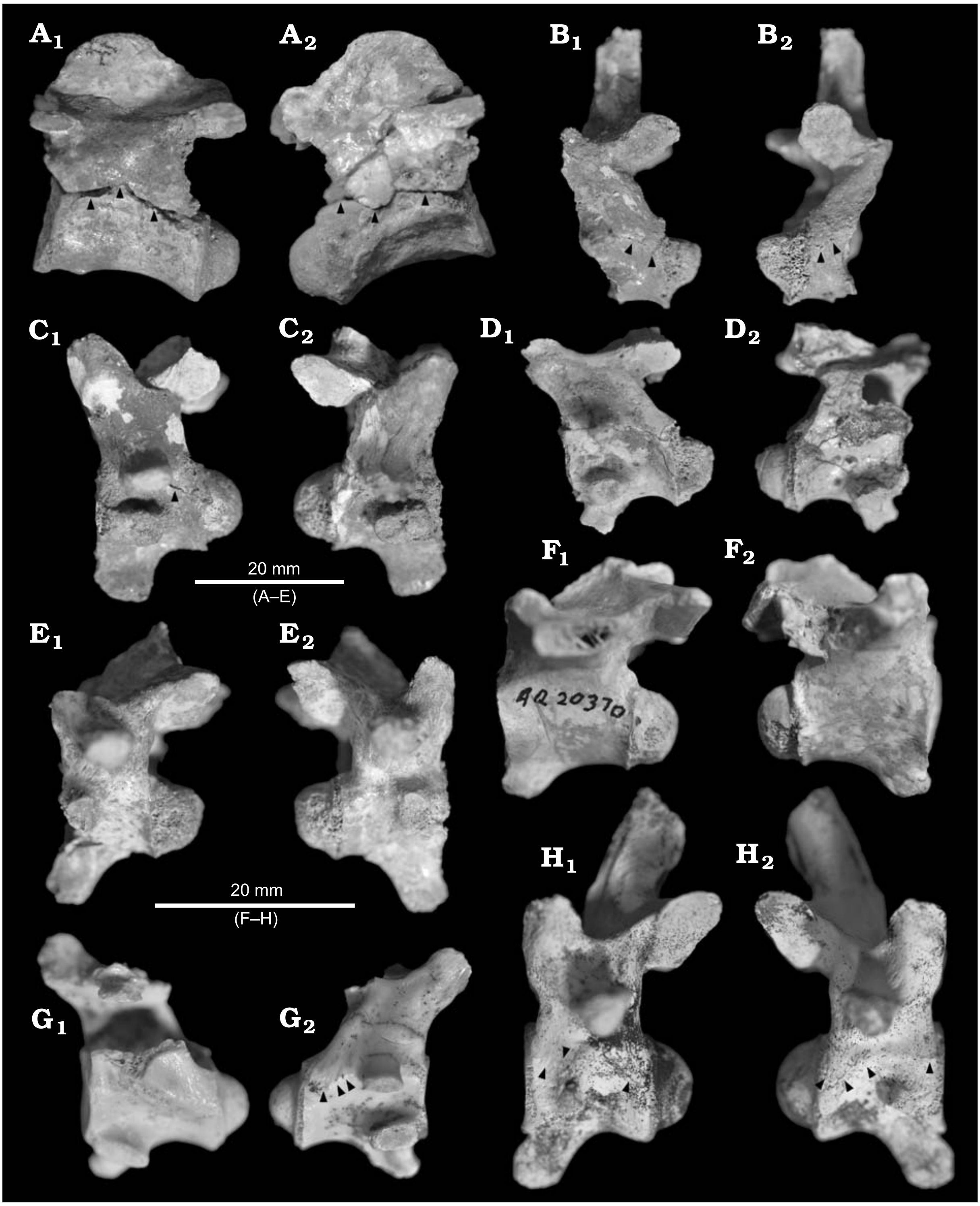

Fig. 2. Vertebrae of mekosuchine crocodile *Mekosuchus whitehunterensis* Willis, 1997; White Hunter Site, Riversleigh World Heritage Area, northwestern Queensland, Australia; late Oligocene. **A**. Axis vertebra (QM F56039). **B**. Third cervical vertebra (QM F56040). **C**. Fourth cervical vertebra (QM F56041). **D**. Sixth cervical vertebra (QM F56042). **E**. Ninth cervical vertebra (QM F56043). **F**. Third thoracic vertebra (QM F56321). **G**. Third cervical vertebra (QM F56320). **H**. Eighth cervical vertebra (QM F56322). Arrows indicate extent of the neurocentral suture; left (A_1–H_1) and right (A_2–H_2) views.

nosed by Willis (1997). The maxilla QM F56046 displays the large disparity of tooth size typical of mekosuchine crocodiles (Fig. 1A_1). QM F56046 further preserves the fifth to tenth maxillary alveoli in deep dentigerous margins with no distinct gap between the sixth and seventh (Fig. 1A_2). The dentary QM F56047 preserves the seventh to seventeenth dentary alveoli along with the remains of the splenial which extends to the level of the seventh alveolus (Fig. 1B_1, B_2). All of these features are diagnostic for *M. whitehunterensis*.

Comparing the maxilla QM F56046 and dentary QM

F56047 to the other mekosuchine species from Riversleigh, there is minimal curvature of the rostrum at the fifth maxillary tooth (Fig. $1A_2$), as opposed to the extensive curvature typical of *Baru wickeni* and *B. huberi* (Willis 1997). Rounded alveoli and teeth are preserved (Fig. $1A_2$, B_2), as opposed to the fully ziphodont dentition of *Quinkana fortirostrum* (Willis 1997). However, both QM F56046 and QM F56047 preserve a short and deep rostrum (Fig. $1A_1$, B_3) characteristic of *M. whitehunterensis* but also *M. sanderi* and *Trilophosuchus rackhami*, the anterior rostra and dentaries for which remain unknown (Willis 1993, 2001). Both *M. sanderi* and *T. rackhami* have been reported only from younger middle Miocene assemblages representing Riversleigh's Faunal Zone C (Willis 1993, 2001). Considering this, QM F56046 and QM F56047 more likely to represent *M. whitehunterensis*, and are tentatively referred to this taxon.

The cervical vertebrae associated with QM F56046 and QM F56047 have features that support the interpretation that they represent a dwarf species. Brochu (1996) reported that ontogenetic closure of the NCS initiates from the posterior-most caudal through to the anterior-most cervical vertebrae. A full or partially closed cervical NCS coincides with the onset of morphological maturity, whether the individual represents a dwarf or larger form. A combination of low snout-vent length and a closed cervical NCS should be significant indicators of dwarf morphology.

The cervical series QM F56039–43 meets both of these criteria. While the complete cervical series is not preserved, known vertebrae indicate a cervical region in the late stages of ontogenetic closure. The posterior ninth and sixth vertebrae are closed (Fig. 2D, E); the fourth and third vertebrae display advanced partial closure (Fig. 2B, C) with more of the NCS visible in the fourth than the third; the axis NSC is open (Fig. 2A). This meets the criterion given by Brochu (1996) for recognising a morphologically mature individual.

The cervical series QM F56039–43 also displays consistently small size (Table 1). Intact centra have a mean anteroposterior length of 19.3 mm. The most complete cranium of *M. whitehunterensis* has an anteroposterior length of ~100 mm (Willis 1997). Together these measures suggest a snout-vent length of approximately 600 mm for this species, given conservative counts of nine cervical and sixteen thoracic-lumbar vertebrae (Salisbury and Frey 2001). Not only does this place *M. whitehunterensis* within the size range of the extant dwarf crocodilian genera *Osteolaminus* and *Paleosuchus,* it indicates a comparatively smaller adult body-size. Population studies of *Osteolaminus* and *Paleosuchus* indicate adult snout-vent lengths greater than one meter are typical in both genera (Campos et al. 2010; Eaton and Link 2011). The vertebrae of cervical series QM F56039–43 are also slightly smaller than those reported for other fossil Cenozoic dwarf taxa, including *Aldabrachampsus dilophus* of the West Indian Ocean and the mekosuchine *Volia athollandersoni* of Fiji (Molnar et al. 2002; Brochu 2006).

The other individual vertebrae corroborate these results. The third thoracic vertebra QM F56321 and third cervical vertebra QM F56320 display short anteroposterior lengths along with a closed NCS (Fig. 2F, G). Fusion of the NCS is nearly complete in QM F56321 (Fig. 2F). Although fusion in the thoracic series is not in itself a sufficient indicator of maturity, it reflects the ontogenetic progression reported by Brochu (1996). The eighth cervical vertebra QM F56322 displays less advanced closure than the ninth cervical vertebra QM F56043, along with smaller proportions (Fig. 2E, H).

A caveat is that QM F56320–22 were collected from apparently older deposits (LSO and Hiatus Sites; late Oligocene) than the cervical series QM F56039–43 (Price is Right Site; early Miocene). That they represent a separate mekosuchine species remains a possibility, although the difference in absolute age of these deposits may be no more than only a few million years. At the very least, QM F56320–22 indicate dwarf crocodiles occurred in Riversleigh faunal assemblages spanning the late Oligocene to early Miocene. Lack of the full cervical series in QM F56039–43 similarly raises the possibility that these may represent multiple individuals, although duplicates of individual vertebrae do not appear to be present. Similar preservation to the maxilla and dentary QM F56046 and QM F56047 and articulation between concurrent vertebrae strongly suggests that these represent a single individual.

The cervical vertebrae are anteroposteriorly narrow compared to those of extant *Crocodylus johnstoni* (Fig. 3), even after accounting for their small size. This suggests that the neck was relatively short in this Riversleigh mekosuchine.

Table 1. Selected measurements (in mm) of mekosuchine vertebrae collected from Riversleigh. Abbreviations: CHant, anterior dorsoventral height of centrum; CHpost, posterior dorsoventral height of centrum; CL, anteroposterior length of centrum; CWant, anterior mediolateral width of centrum; CWpost, posterior mediolateral width of centrum; NAH, dorsoventral height of nerual arch; ZL, anteroposterior length of zygapophyses; ZWant, mediolateral width of anterior zygapophyses; ZWpost, mediolateral width of posterior zygapophyses.

Specimen	CL	CWant	CHant	CWpost	CHpost	ZL	ZWant	ZW-post	NAH
QM F56039	26.4	11.9	13.7	15.6	12.8	28.7	15.4	–	10.7
QM F56040	–	–	–	13.4	11.8	–	–	19.2	7.8
QM F56041	19.3	14.7	12.1	15.6	11.2	20.2	24.8	19.3	7.7
QM F56042	20.3	10.1	11.1	12.9	10.3	–	–	–	7.1
QM F56043	18.2	12.4	12.1	14.8	10	20.2	24.8	23.9	7.7
QM F56320	16.7	9.1	8.5	10.6	9.8	–	–	–	7.5
QM F56321	17.4	10.6	9.1	9.4	9.3	18.9	20.3	–	6.2
QM F56322	16.9	11.2	11.6	11.3	10.9	17.3	19.6	19	6.2

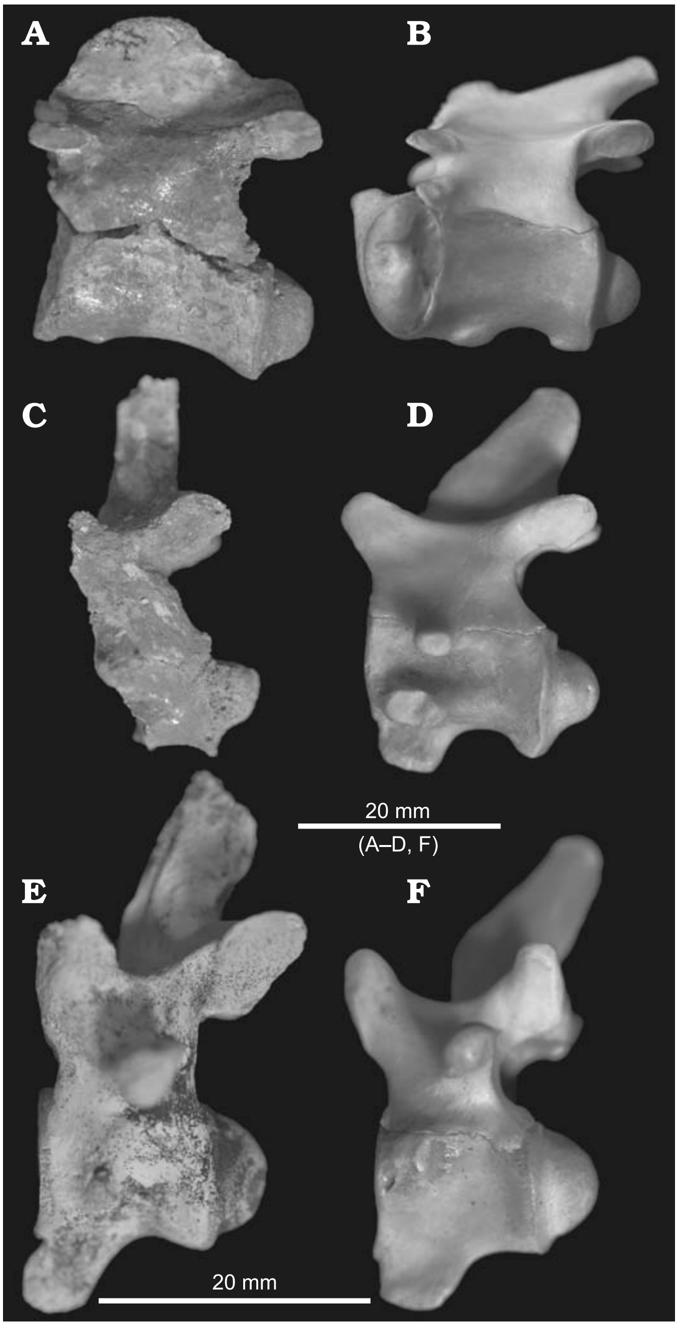

Fig. 3. Vertebral morphology of mekosuchine crocodile *Mekosuchus whitehunterensis* Willis, 1997 (**A**, **C**, **E**) from White Hunter Site, Riversleigh World Heritage Area, northwestern Queensland, Australia, late Oligocene compared with *Crocodylus johnstoni* Krefft, 1873 (**B**, **D**, **F**) from upper Herbert River, northeastern Queensland, Australia, late Pleistocene–Holocene. Axis vertebrae (**A**, QM F56039; **B**, AR 17683). Third cervical vertebrae (**C**, QM F56040; **D**, AR 17683). Eighth cervical vertebrae (**E**, QM F56322; **F**, AR 17683). All in left view.

The tall spinous process of the axis vertebra QM F56039 displays a dorsoposterior slope typical of crocodyloids (Fig. 3A, B). In shape, however, it is closer to the broad keel of alligatoroids than the narrow process of crocodyloids (Brochu 1999).

The third cervical vertebra QM F56040 and eighth cervical vertebra QM F56322 do not preserve the full height of the spinous process (Fig. 2B, H). The preserved bases indicate that the height of the process increased in the posterior cervical vertebrae, conforming to the bracing patterns of extant crocodilians excluding gharials (Salisbury and Frey 2001; Salisbury et al. 2006). Compared to the spinous process of the axis vertebra QM F56039 and those of extant *Crocodylus* of comparable size such as *C. johnstoni* and species of *Osteolaminus* (Fig. 3), however, the height of the processes in QM F56040 and QM F56322 must have been considerable. The spinous processes also show less posterodorsal inclination than they do in species of *Crocodylus* (Fig. 3C–F). This perpendicular aspect is more pronounced in the anterior cervicals than in the posterior ones. The angle formed between spinous process and centrum of the third cervical vertebra QM F56040 is approximately 16° greater than the same angle in extant *C. johnstoni* in lateral view. Compare this to the eighth cervical vertebra QM F56322 where the angle between spinous process and centrum is only 8° greater than the same angle in *C. johnstoni*.

These features indicate that this Riversleigh mekosuchine, despite its small size, possessed large and powerful epaxial musculature of the neck. Increased insertion area between sites of homologous musculature, evident between the axis vertebra QM F56039 and *C. johnstoni* (Fig. 3A, B, Table 2), correlates with increased cross-sectional area of musculature and muscle force (Kardong 2006; Snively and Russell 2007b). Spinous processes of the third cervical vertebra QM F56040 and eighth cervical vertebra QM F56322 ostensibly display lower surface area than *C. johnstoni* (Table 2). However, because the spinous processes of QM F56039, QM F56040, and QM F56322 are incomplete, measureable surface areas are effectively underestimates. The spinous processes of QM F56040 and QM F56322 appear to gain in dorsoventral height what they lose in anterioposterior length. Coupled with their perpendicular aspect, this indicates a concomitant increase in the height and therefore cross-sectional area of the epaxial musculature, particularly the M. transversospinalis capitis and M. transversospinalis cervicis (Frey 1988; Organ 2006; Tsuihiji 2007; Schwarz-Wings et al. 2009). This is supported by well developed lateral attachment scars on the spinous process visible in both QM F56040 and QM F56322 (Fig. 3C, E).

Enlarged epaxial neck musculature can be interpreted in terms of feeding behaviours including those used to segment large carcasses into smaller edible portions (Webb and Manolis 1989). Two methods are observed in extant crocodilians. The first is the iconic death-roll, which generates torsion shear-forces resulting from whole-body rotation. The second involves lateral shear-force generated by shaking of the head and neck. Various rotating and shaking motions of

Table 2. Measured surface areas (in mm^2) of the spinous process in vertebrae referred to *Mekosuchus whitehunterensis* compared to those in *Crocodylus johnstoni* (AR 17683).

Specimen	surface area *Mekosuchus*	surface area *Crocodylus*
QM F56039	171.1	99.8
QM F56040	77.9	124
QM F56322	84.3	133

the cranium and neck are also used to manipulate prey items in the jaws (Webb and Manolis 1989; Fish et al. 2007).

The small size of this Riversleigh mekosuchine imposes a corresponding limit on the shear-force it could generate by rolling. Shear-force from rolling predicted for a 1.5 m individual is one to two orders of magnitude less for that that of a three to four meter crocodilian under most rotational velocities (Fish et al. 2007). While rolling can be induced in hatchlings, it has not been observed in relation to their general feeding behaviours; shaking behaviours characterise the feeding of these small-bodied individuals (Davenport et al. 1990).

Enlarged epaxial neck musculature would assist de-fleshing by shaking. These muscles are the primary flexors, extensors, and stabilisers of the cranium with respect to the atlas. In tandem with the musculature of the pectoral girdle, they also flex and extend the cervical vertebrae against the thoracic vertebrae (Frey 1988; Salisbury and Frey 2001). In both instances this includes the lateral movements that are part of shaking behaviours. Increased cross-sectional area would increase the force that could be generated by such motions, as well as the way in which these motions could be applied.

This has interesting implications for the terrestrial habitus attributed to mekosuchines like *M. whitehunterensis* (Willis 1997). In addition to the limitations of small size, the crocodilian death-roll is potentially inhibited and more self-damaging in a terrestrial environment. The internally generated rotation of the death-roll is effective in the aquatic environment because the surrounding water imposes negligible reaction forces to the motion of the axial body and upon appendages of the crocodile (Fish et al. 2007). A terrestrial death-roll would induce considerable ground reaction forces opposed to the motion of the axial body and could result in limb damage. Enlarged epaxial neck musculature again provides a clear advantage in such a setting. Higher force generation by the enlarged neck muscle would facilitate de-fleshing via lifting of the cranium to pull apart carcass restrained by gravity, a pattern interpreted to have been common in terrestrial archosaurian carnivores (Snively and Russell 2007a, b).

In a terrestrial setting, either as primary habitat or due to extended overland migration between water sources (Kofron 1993; Dever et al. 2002; Brito et al. 2011; Velo-Antón et al. 2014), this would allow this Riversleigh mekosuchine to engage in scavenging or active predation of disproportionately large prey in relation to its body-size. Scavenging in particular, offers a dwarf mekosuchine food sources well in excess of its body-size and is congruent with the cryptic behaviour observed in extant dwarf crocodilians (Webb and Manolis 1989).

The perpendicular aspect of the spinous processes may also relate to feeding through the biomechanics of the cervical vertebral column itself. The vertebrae of the cervical region in crocodilians operate as a single unit braced primarily against ventral flexure by contacting cervical costae (Salisbury and Frey 2001). The perpendicular aspect of the anterior cervical spinous processes potentially reinforces the cervical column further dorsally through contact between the processes, forming a solid support against which the epaxial neck musculature could extend the cranium. Alternately any contact between spinous processes may be a biomechanical consequence of enlarging the epaxial neck musculature. This is not to say that the neck was immobile. The inclination of the posterior cervical vertebrae would still permit pivoting between the cervical and thoracic regions (Salisbury and Frey 2001). The size of the spinous processes of the vertebrae described here may well reflect a compromise between the advantages of enlarged musculature and the need for cervical mobility.

The diagnosis of *Mekosuchus inexpectatus* mentions strong spinous processes of the cervical vertebrae (Balouet and Buffetaut 1987). Willis (1997) left this feature out of the amended generic diagnosis because these structures were not known for the other species in his analysis. The new specimens described here suggest that expanded perpendicular spinous processes are characteristics for at least some species of *Mekosuchus*. These findings are also congruent with the orientation of the cervical musculature observed by Willis (1993) in *T. rackhami* and a cervical vertebra described for *V. athollandersoni* (Molnar et al. 2002). Willis (1993) suggested that the ventrally-directed musculature provided an extended lever arm for lifting the cranium. This raises the possibility that the vertebral morphology described here is part of a broader morphological complex characteristic of mekosuchine crocodiles in general, a possibility that warrants further investigation, particularly in relation to the larger, purportedly terrestrial species of *Quinkana* (Willis 1997).

Conclusions

Vertebrae from Riversleigh demonstrate that dwarf morphology was a feature of at least one Oligo-Miocene mekosuchine crocodile species. The vertebrae display advanced ontogenetic fusion of the NCS which indicates that despite their small size, they were adults distinctly smaller in snout-vent length than extant dwarf crocodilians. Associated cranial materials suggest that these vertebrae are referable to *Mekosuchus whitehunterensis*. These vertebrae also preserve spinous processes that indicate a greater mass of the epaxial musculature in the neck. This is interpreted as an adaptation for cranial-cervical de-fleshing in contrast to the death-roll strategies known to be employed by larger living crocodiles. It is also possible that these adaptations in a terrestrial context would have facilitated cranial lifting as another mechanism for dismembering large terrestrial prey.

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