Dwarfism and Feeding Behaviours in Oligo-Miocene Crocodiles from Riversleigh, Northwestern Queensland, Australia

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

MICHAEL STEIN, MICHAEL ARCHER, and SUZANNE J. HAND


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 crocodylians (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 crocodylian 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 palaeontological 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-
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 vertebra 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 mm² 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). Partial closure is evident at the anterior and posterior-most ends of the NCS with respect to the long axis of the centrum in lateral view. The NCS displays the open state.

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 posteriordorsally. The hypapophysis is elongate and inclines more steeply anteroventrally 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 anteroventrally. 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-
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 posteriordorsally 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-
nosed by Willis (1997). The maxilla QM F56046 displays the large disparity of tooth size typical of mekosuchine crocodiles (Fig. 1A1). QM F56046 further preserves the fifth to tenth maxillary alveoli in deep dentigerous margins with no distinct gap between the sixth and seventh (Fig. 1A2). 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. 1B1, B2). All of these features are diagnostic for *M. whitehunterensis*. Comparing the maxilla QM F56046 and dentary QM
Table 1. Selected measurements (in mm) of mekosuchine vertebrae collected from Riversleigh. Abbreviations: CL, anteroposterior length of centrum; CHpost, posterior dorsoventral height of centrum; CWpost, posterior mediolateral width of centrum; CWpost, posterior mediolateral width of centrum; ZL, anteroposterior length of zygapophyses; ZWant, mediolateral width of anterior zygapophyses; ZW-post, mediolateral width of posterior zygapophyses.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>CL</th>
<th>CWant</th>
<th>CHant</th>
<th>CWpost</th>
<th>CHpost</th>
<th>ZL</th>
<th>ZWant</th>
<th>ZW-post</th>
<th>NAH</th>
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<tr>
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<td>11.9</td>
<td>13.7</td>
<td>15.6</td>
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<td>28.7</td>
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<td>10.7</td>
</tr>
<tr>
<td>QM F56040</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>13.4</td>
<td>11.8</td>
<td>–</td>
<td>–</td>
<td>19.2</td>
</tr>
<tr>
<td>QM F56041</td>
<td>19.3</td>
<td>14.7</td>
<td>12.1</td>
<td>15.6</td>
<td>11.2</td>
<td>20.2</td>
<td>24.8</td>
<td>19.3</td>
<td>7.7</td>
</tr>
<tr>
<td>QM F56042</td>
<td>20.3</td>
<td>10.1</td>
<td>11.1</td>
<td>12.9</td>
<td>10.3</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
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<td>18.2</td>
<td>12.4</td>
<td>12.1</td>
<td>14.8</td>
<td>10</td>
<td>20.2</td>
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</tr>
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<td>8.5</td>
<td>10.6</td>
<td>9.8</td>
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<td>11.6</td>
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<td>17.3</td>
<td>19.6</td>
<td>19</td>
<td>6.2</td>
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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 alligato-roids 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 pos-
terodorsal 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 lat-
eral 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 cro-
codilians. 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>
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<tr>
<th>Specimen</th>
<th>surface area Mekosuchus</th>
<th>surface area Crocodylus</th>
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<tr>
<td>QM F56039</td>
<td>171.1</td>
<td>99.8</td>
</tr>
<tr>
<td>QM F56040</td>
<td>77.9</td>
<td>124</td>
</tr>
<tr>
<td>QM F56322</td>
<td>84.3</td>
<td>133</td>
</tr>
</tbody>
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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
dividual 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 gen-
eral feeding behaviours; shaking behaviours characterise
the feeding of these small-bodied individuals (Davenport et
al. 1990).

Enlarged epaxial neck musculature would assist de-flesh-
ing by shaking. These muscles are the primary flexors, exten-
sors, 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 tho-
racic 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 croco-
dilian death-roll is potentially inhibited and more self-damag-
ing in a terrestrial environment. The internally generated ro-
tation 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 archo-
saurian 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 disproportio-
nately 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 cer-
vical vertebral column itself. The vertebrae of the cervical
region in crocodilians operate as a single unit braced pri-
marily 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 be-
tween 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 re-
gions (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 muscula-
ture and the need for cervical mobility.

The diagnosis of *Mekosuchus inexpectatus* mentions
strong spinous processes of the cervical vertebrae (Balout
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 perpendic-
ular 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 de-
scribed 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 com-
plex 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 mor-
phology was a feature of at least one Oligo-Miocene meko-
suchine 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 cra-
nial materials suggest that these vertebrae are referable to
*Mekosuchus whitehunterensis*. These vertebrae also pre-
serve 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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...
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