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Early to middle Pleistocene occurrences of *Litoria*, *Neobatrachus* and *Pseudophryne* (Anura) from the Nullarbor Plain, Australia: first frogs from the "frog-free zone"

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Abstract

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Frogs have the least understood fossil record of all major vertebrate groups in Australia. Here we report on pelvic remains of three Pleistocene frog species from the Nullarbor Plain, a large region of Australia where no living or fossil frogs had previously been discovered. One ilium, characterised by a small acetabular fossa with an indistinct peripheral rim, a broad dorsal prominence and enlarged supra-acetabular zone, is recognised here as representative of a new species of hylid, *Litoria lundeliusi* sp. nov. Three other ilia bear the hallmark generic attributes of the small myobatrachid *Pseudophryne*, two species of which co-occur today over much of southwestern Australia. A second larger myobatrachid is the best represented of the three species, and its ilial morphology matches that of the extant *Neobatrachus sudelli*. All three species were present in the early Pleistocene, but only *N. sudelli* is recorded in the middle Pleistocene. The loss of *Litoria* and *Pseudophryne* would be consistent with the disappearance of significant bodies of free water from the region, but the cause of the apparent extirpation of *N. sudelli*, which inhabits arid parts of Australia today, remains a mystery.

Keywords Hylidae, *Litoria lundeliusi*, Myobatrachidae, *Neobatrachus sudelli*, *Pseudophryne*, biogeography, Cenozoic, fossil frogs.

Introduction

To a palaeontologist nothing quite matches the mix of confusion and excitement that follows the discovery of fossils that are "not supposed to be there". Few palaeontologists seem to have done this as regularly as Thomas Hewitt Rich, so it is with pleasure that we honour Tom here by describing the first frog remains from the Nullarbor Plain of south-central Australia. The Nullarbor today is one of the largest regions of Australia that frogs are not known to inhabit (fig. 1).

The Nullarbor frogs are part of an early to middle Pleistocene vertebrate assemblage retrieved from Leaena's Breath Cave, one of three caves collectively named the Thylacoleo Caves that were discovered by cavers in 2002. High species diversity and remarkably complete preservation are hallmarks of the assemblage, which fills a significant gap in our understanding of the Quaternary biogeography of southern Australia (Prideaux et al., 2007). Leaena's Breath Cave is the only known Australian vertebrate locality that spans the early to middle Pleistocene boundary. Excavations conducted in 2009, 2011 and 2013 removed approximately 15 tonnes of bone-laden silt from two pits (A and B) in the floor of Leaena's Breath Cave. Scattered among the hundreds of thousands of small mammal, reptile and passerine bird bones were 17 partial frog ilia (hip bones) allocated herein to *Litoria lundeliusi* sp. nov., *Pseudophryne* sp. indet. and *Neobatrachus sudelli*. In this paper we describe and compare the new material and consider the palaeoenvironmental implications of their former presence on the "treeless" and now largely waterless plain.

The identification of Australian fossil frogs is currently based entirely upon the form of the ilium, which is particularly large and distinctive in frogs given its importance as an attachment area for the hopping musculature. A combination of morphology and size can be readily used to diagnose frog ilia to genus or species level (Tyler, 1976, 2010; Hocknull, 2005; Price and Sobbe 2005). So far there

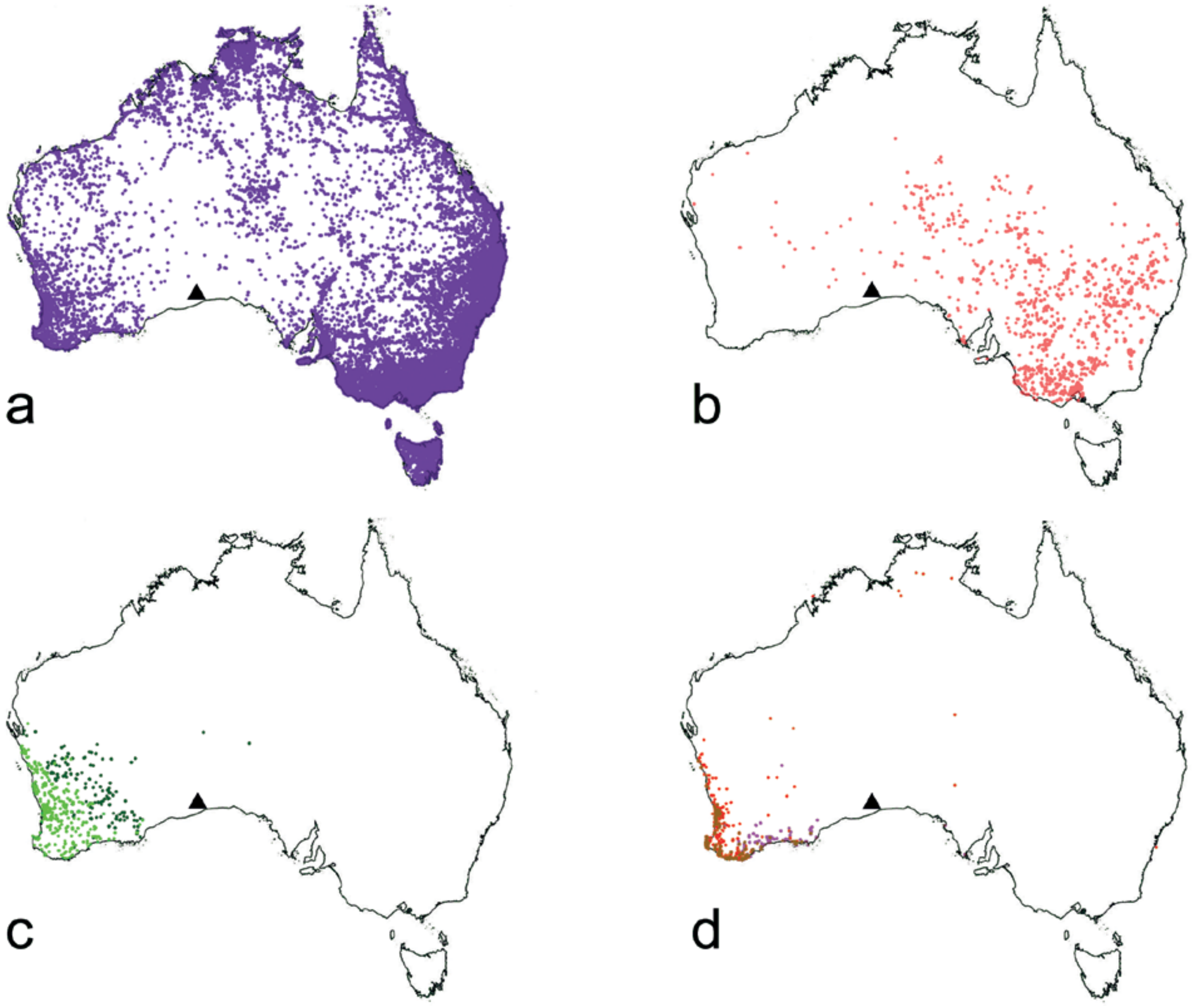

Figure 1. Map of Australia showing modern occurrence records extracted from the Atlas of Living Australia (www.ala.org.au) and location of Leaena's Breath Cave (black triangle). **a**) Anura. **b**) *Neobatrachus sudelli*. Note that the two most northwestern records may represent *N. aquilonius* (J. D. Roberts, pers. comm., 27 June 2015). **c**) *Pseudophryne guentheri* (light green) and *P. occidentalis* (dark green). **d**) *Litoria adelaidensis* (red), *L. cyclorhyncha* (purple) and *L. moorei* (light brown).

have been no comparative studies of other skeletal components, although we have recovered elements such as vertebrae and radioulnae from Leaena's Breath Cave, which may have some future utility when the comparative groundwork is eventually done.

Materials and Methods

Over the course of three weeks in each of 2009, 2011 and 2013, sediment excavated from the floor of Leaena's Breath Cave was removed from the cave, dry screened and then wet screened prior to transport to the Flinders University Palaeontology Laboratory. Sieve residue was then hand-picked for small vertebrate bones. All of the fossil specimens are deposited in the Palaeontology Collection of the Department of Earth and Planetary Sciences, Western Australian Museum, Perth (specimen prefix WAM). Comparative extant material is registered in the Herpetology collection of the South Australian Museum, Adelaide (specimen prefix SAMA R). Descriptive terminology of the ilium (fig. 2) follows Tyler (1976).

Systematic Palaeontology

Anura Duméril, 1806

Hylidae Rafinesque, 1815

Litoria Tschudi, 1838

Litoria lundeliusi sp. nov.

Zoobank LSID. http://zoobank.org/urn:lsid:zoobank.org:act:2ECD98EC-4924-4E5D-83BC-A7CCBC098199.

Holotype. WAM 09.3.264. An incomplete right ilium lacking the proximal portion of the acetabular fossa and the extreme superior margin of the superior acetabular expansion (figs. 3A–B).

Etymology. Named in honour of Ernest L. Lundelius, pioneer Quaternary vertebrate palaeontologist who initiated the first Nullarbor cave excavations in 1955 and 1964, before returning in 2009 to discover the first fossil frog specimen known from the region.

Type locality. The holotype originated from infill sedimentary unit 3 within the main chamber of Leaena's Breath Cave, Nullarbor Plain, southeastern Western Australia (fig. 1). Specifically, it was sieved from sediment excavated from LBC Pit A, quadrat 4, depth 65–70 cm in 2011 by a team led by GJP. Precise location data for the site are registered with the Department of Earth and Planetary Sciences, Western Australian Museum, Perth. Fine-grained sediments in unit 3 are of reversed magnetic polarity, which along with overall species composition of the assemblage, indicate an early Pleistocene age (Matuyama Reversed Chron) (Prideaux et al., 2007). This falls within the Naracoortean land mammal age (Megirian et al., 2010).

Diagnosis. Recognised as a species of *Litoria* due to presence of a well-developed pre-acetabular zone. Distinguished from other species on the following attributes. Anterior border is broad and evenly curved and terminates inferiorly parallel to the slightly raised acetabular rim. The dorsal prominence is broad and distinctly raised. It extends from a position above the middle of the acetabulum, distally to above the commencement of the preacetabular zone. There is no dorsal protuberance. The ilial shaft bears a short remnant of a very narrow flange curving medially and about 100 microns deep. The shaft depth is equivalent to approximately two thirds of the depth of the acetabular fossa.

Comparison with other species. The ilial characteristics of *L. adelaidensis* (fig. 3C) including the large acetabular fossa with a conspicuous peripheral rim, narrow dorsal prominence and reduced supra-acetabular zone, distinguish it from *L. lundeliusi*. The ilium of *L. lundeliusi*, which is presumed to be that of an adult given the very short nature of the subadult stage, is less than half the size of those of the other two southern species, *L. cyclorhyncha* and *L. moorei*. *L. lundeliusi* is distinguished from *L. rubella* sensu stricto (fig. 3D) by having a broader pre-acetabular zone, a deeper and more extensive acetabular fossa, a more extensive supra-acetabular region, and a curved and narrow ilial ridge, which may be extensive in complete specimens. *L. lundeliusi* also lacks a dorsal prominence. Future comparisons should be made, however, with *L. rubella* sensu lato, which is currently under taxonomic revision and will soon be divided into several species. This species complex is extensively distributed through Australia and southern New Guinea, and is renowned for its capacity to colonise diverse and, for a hylid, relatively arid habitats.

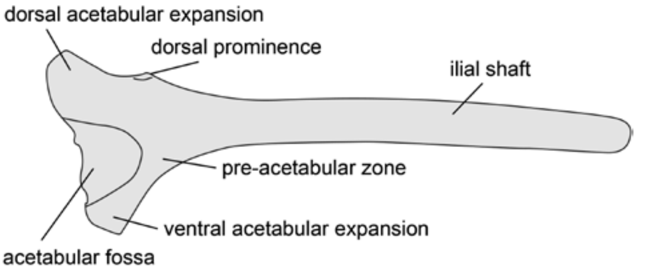

Figure 2. Anatomical features of the frog ilium mentioned in the text. Adapted from Tyler (1976).

Myobatrachidae Schlegel, 1850

Neobatrachus Günther, 1873

Neobatrachus sudelli (Lamb, 1911)

Referred specimens. Leaena's Breath Cave, ilia: WAM 09.3.260, WAM 09.3.268 (unit 1); WAM 09.3.262, WAM 09.3.272 (unit 2); WAM 09.3.261, WAM 09.3.263, WAM 09.3.265, WAM 09.3.267, WAM 09.3.269, WAM 09.3.270, WAM 09.3.271, WAM 09.3.273, WAM 09.3.276 (unit 3).

Locality. The referred specimens originated from infill sedimentary units 1–3 within the main chamber of Leaena's Breath Cave, Nullarbor Plain, southeastern Western Australia (fig. 1; table 1). Units 1–2 are of normal magnetic polarity (Brunhes Normal Chron) and are capped in places by speleothem samples dated to ca 400,000 years, so are middle Pleistocene in age (Prideaux et al., 2007). This falls within the Naracoortean land mammal age (Megirian et al., 2010). Unit 3 is of early Pleistocene age.

Remarks. The specimens are identified as representing a species of *Neobatrachus* because they possess a very large and irregularly-shaped dorsal prominence, which varies markedly intraspecifically within this genus (figs. 3E–H; Tyler, 1976, 1985). Congeners are distinguished by differences in the height of the dorsal protuberance of the ilium, its shape, and its position on the ilial shaft. In WAM 09.3.260 the dorsal prominence bears an elongated and shallow vertical incision, a well-developed pre-acetabular zone and a broad anterior border (fig. 3H). Such a feature has not been reported in any other anuran ilium. The superior acetabular expansion inclines at approximately 45° to the ilial shaft. With this exception, the features expressed by this specimen and each of the Nullarbor *Neobatrachus* ilia fall within the range of variation expressed by extant specimens of *N. sudelli*, into which *N. centralis* has now been synonymised (Roberts, 2010).

Figure 3. Pleistocene frog ilia from Leaena's Breath Cave (prefix WAM) compared with modern specimens (prefix SAMA). **a**) WAM 09.3.264. Right ilium of holotype of *Litoria lundeliusi* sp. nov. from Leaena's Breath Cave (unit 3). **b**) WAM 09.3.264. Enlargement of acetabular region of holotype of *Litoria lundeliusi* sp. nov. **c**) SAMA R68398. Representative left ilium of *Litoria adelaidensis*. **d**) SAMA R68399. Representative right ilium of *Litoria rubella* sensu stricto. **e–h**) Representative ilia of *Neobatrachus sudelli* highlighting extreme divergence in the form of the dorsal prominence. **e**) WAM 09.3.265. **f**) WAM 09.3.261. **g**) WAM 09.3.269. **h**) WAM 09.3.273. **i**) Right ilium of *Pseudophryne* sp. indet.

Table 1. List of ilial specimens from Leaena's Breath Cave, Nullarbor Plain, Western Australia.

WAM No.	Species	Collection details	Unit
09.3.260	*Neobatrachus sudelli*	LBC.A2.5–10cm	Unit 1
09.3.268	*Neobatrachus sudelli*	LBC.15–20cm	Unit 1
09.3.262	*Neobatrachus sudelli*	LBC.B4.40–45cm	Unit 2
09.3.272	*Neobatrachus sudelli*	LBC.A1.40–45cm	Unit 2
09.3.267	*Neobatrachus sudelli*	LBC.A4.65–70cm	Unit 3
09.3.269	*Neobatrachus sudelli*	LBC.A4.75–80cm	Unit 3
09.3.261	*Neobatrachus sudelli*	LBC.A4.80–85cm	Unit 3
09.3.276	*Neobatrachus sudelli*	LBC.B6.85–90cm	Unit 3
09.3.263	*Neobatrachus sudelli*	LBC.B2.95–100cm	Unit 3
09.3.265	*Neobatrachus sudelli*	LBC.B2.105–110cm	Unit 3
09.3.271	*Neobatrachus sudelli*	LBC.B2.105–110cm	Unit 3
09.3.273	*Neobatrachus sudelli*	LBC.B2.105–110cm	Unit 3
09.3.270	*Neobatrachus sudelli*	LBC.B1.120–125cm	Unit 3
09.3.264	*Litoria lundeliusi* sp. nov.	LBC.A4.65–70cm	Unit 3
09.3.274	*Pseudophryne* sp. indet.	LBC.B2.70–75cm	Unit 3
09.3.266	*Pseudophryne* sp. indet.	LBC.A4.80–85cm	Unit 3
09.3.275	*Pseudophryne* sp. indet.	LBC.B1.120–125cm	Unit 3

Pseudophryne Fitzinger, 1843

Pseudophryne sp. indet.

Referred specimens. Leaena's Breath Cave, ilia: WAM 09.3.266, WAM 09.3.274, WAM 09.3.275 (unit 3).

Locality. The three specimens originated from infill sedimentary unit 3 within the main chamber of Leaena's Breath Cave, Nullarbor Plain, southeastern Western Australia (fig. 1; table 1). Unit 3 is of early Pleistocene age (Prideaux et al., 2007).

Remarks. A conspicuous feature is the curvature extending from the ventral face of the ilial shaft to the pre-acetabular zone, forming a perfect quadrant. The acetabulum is large, with a slightly raised, narrow peripheral rim. The dorsal prominence and protuberance are only slightly elevated, and the dorsal acetabular expansion inclines to the iliac shaft at approximately 30° (fig. 3i). The specimens are indistinguishable from extant specimens of *Pseudophryne guentheri* in ilial morphology, but no skeletal material of the other southwestern congener, *P. occidentalis*, was available for study here. Until comparisons can be made with ilial specimens of *P. occidentalis*, the Leaena's Breath Cave specimens are referred to *Pseudophryne* sp. indet.

Discussion

Comparative skeletal material has been isolated for only a limited number of the 150 or so extant species of *Litoria*. This includes the three southern species, *L. adelaidensis*, *L. cyclorhyncha* and *L. moorei*. Although there are no valid taxonomic grounds for excluding other extant species a priori as the source of WAM 09.3.264 given the potential for climate-driven range shifts over time, we feel that the best course of action at present is to recognise WAM 09.3.264 as representative of a new species, *L. lundeliusi*. A close relationship between ilial length and snout-to-vent length (SVL) has been demonstrated in several Australian species, e.g., a study of the hylid *Cyclorana australis* showed a linear relationship throughout ontogeny and a r^2 value of 0.95 (Walker, 1994). Thus, SVL can be estimated with accuracy from the length of complete isolated ilia. Judging from its almost complete ilial length, SVL for WAM 09.3.264 would have been within the range of 25–30 mm. The only southern species close to it in size is *L. adelaidensis* (SVL 34–47 mm). *Litoria cyclorhyncha* and *L. moorei* are much larger by comparison; adults possess SVL ranges of 47–80 mm. None of these three extant species are known to occur closer than 500 km to the west of the Thylacoleo Caves area today (Tyler and Doughty, 2009). The closest occurrence, according to the Atlas of Living Australia (www.ala.org.au), is a record of *L. cyclorhyncha* from near Balladonia on the western edge of the Eucla Basin (fig. 1).

The Nullarbor fossil ilia cannot be distinguished from ilial specimens of the extant *Pseudophryne guentheri*, which occupies much of southwestern Australia extending to Balladonia on the western edge of the Eucla Basin. However, *P. occidentalis* is sympatric with *P. guentheri* over much of its range (fig. 1), and has also been recorded at Balladonia. No skeletal material has been isolated from any specimens of *P.*

occidentalis, which remains a candidate species for the Nullarbor fossil specimens.

The Nullarbor Plain must have been characterised by at least seasonally moist conditions during the early Pleistocene when unit 3 accumulated, because of the ephemeral pools required for breeding by the species of *Litoria* and *Pseudophryne*. DNA-based divergence-time estimates for many southwestern Australian taxa suggest that those requiring wetter conditions became separated from their eastern counterparts due to the increasingly arid Nullarbor region by the middle Miocene, with *Litoria* and *Pseudophryne* purportedly among the last to diverge 12–8 million years ago (Roberts and Maxson, 1985; Rix et al., 2014). Establishing that both genera were represented on the Nullarbor closer to 1 million years ago suggests that the role played by the region as a biogeographic barrier or filter may not be as straightforward as has been conceived.

Only *Neobatrachus sudelli* is represented in the middle Pleistocene (units 1–2) of Leaena's Breath Cave, which is consistent with its capacity to occupy arid regions today (fig. 1). Moreover, extant specimens have been collected from three locations along the northern periphery of the Nullarbor Plain (fig. 1). It is difficult to fathom why *N. sudelli* would not have persisted on the Nullarbor to the present day, given comparable rainfall to bordering areas and clayey soils of sufficient thickness into which individuals might conceivably burrow and aestivate exist in the lower-lying dongas. Rapid drainage of water into the underlying limestone may be a factor, but there are no obvious climatic or geomorphological reasons to posit that this may have increased significantly over the past few hundred thousand years. Morever, *N. sudelli* copes well in lower-rainfall areas where surface water disappears relatively quickly after sporadic rainfall events. Data from other Nullarbor vertebrate deposits may eventually shed some light on this conundrum.

Acknowledgements

Well over 50 individuals, some paid, most unpaid, have been involved in the Leaena's Breath Cave component of the Thylacoleo Caves research program. We greatly appreciate their efforts in excavating over 15 tonnes of sediment, dragging hundreds of sediment bags up a precarious pile of teetering boulders, and lugging them up a 20-m vertical solution pipe, before sieving out the bones. In particular, we offer our deepest gratitude to LBC stalwarts Grant Gully, Carey Burke, Lindsay Hatcher, Clay Bryce, Mark Norton and the late Paul Devine. Paul not only discovered LBC but mapped it, found most of the best specimens and worked longer hours underground than anyone else. The most time-consuming and arduous process, however, has been the thousands of hours of assiduous hand-picking of a small mountain of sieve residue for small vertebrate remains undertaken by staff, students and mostly volunteers in the Flinders University Palaeontology Laboratory. We sincerely thank John Harper for leading the way on this often thankless task and for isolating most of the 17 coveted frog ilia himself from the hundreds of thousands of other small vertebrate bones. We also thank Grant Gully for drafting the figures and assisting with obtaining SEM images. The Thylacoleo Caves research program was funded by National Geographic, Flinders University, the Western Australian Museum, South Australian Museum and Geological Survey of Western Australia, and an Australian Research Council Future Fellowship grant (FT130101728) to GJP. Finally, we gratefully acknowledge the insightful reviews of Chris Bell and Dale Roberts, whose suggestions markedly improved the paper.

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