Crayfish bio-gastroliths from eastern Australia and the middle Cretaceous distribution of Parastacidae

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Abstract

Fossil crayfish are typically rare, worldwide. In Australia, the strictly Southern Hemisphere clade Parastacidae, while ubiquitous in modern freshwater systems, is known only from sparse fossil occurrences from the Aptian–Albian of Victoria. We expand this record to the Cenomanian of northern New South Wales, where opalized bio-gastroliths (temporary calcium storage bodies found in the foregut of pre-moult crayfish) form a significant proportion of the fauna of the Griman Creek Formation. Crayfish bio-gastroliths are exceedingly rare in the fossil record but here form a remarkable supplementary record for crayfish, whose body and trace fossils are otherwise unknown from the Griman Creek Formation. The new specimens indicate that parastacid crayfish were widespread in eastern Australia by middle Cretaceous time, occupying a variety of freshwater ecosystems from the Australian–Antarctic rift valley in the south, to the near-coastal floodplains surrounding the epeiric Eromanga Sea further to the north.

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1. Introduction

Decapod crustaceans are a diverse arthropod group with ~15 000 named species among more than 170 families (Crandall *et al.* 2009). Fossil decapods, however, are generally rare (Pagani *et al.* 2011). The first members of this group can be traced to the Devonian Period (Feldmann & Schweitzer, 2010; Gueriau *et al.* 2014), although molecular clock estimates indicate an early Silurian (~430 Ma) origin for the group, with all major infraorders represented by late Carboniferous time (Crandall *et al.* 2009).

Crayfish – freshwater decapod crustaceans (Astacidea Latreille, 1802) – are unusual in that they do not inhabit marine conditions typical of decapods (Bliss, 1968). Although crayfish fossils are rare (Feldmann & Pole, 1994; Babcock *et al.* 1998; Taylor *et al.* 1999; Shen *et al.* 2001; Martin *et al.* 2008; Feldmann *et al.* 2011), their record extends to the Pennsylvanian, suggesting an early Carboniferous origin, prior to the Pangaean break-up (Hasiotis, 2002). After the break-up, three crayfish families diverged across Laurasia and Gondwana: Cambaridae Hobbs, 1942 and Astacidae Latreille, 1802 (Northern Hemisphere) and Parastacidae Huxley, 1879 (mostly Southern Hemisphere, but see Feldmann *et al.* 2011) (Hasiotis, 2002). The majority of fossil evidence for crayfish comes from their traces, especially burrows (Hasiotis & Mitchell, 1993; Babcock *et al.* 1998; Hasiotis *et al.* 1998), although body fossils are also known (e.g. Garassino, 1997; Taylor *et al.* 1999; Garassino & Krobicki, 2002; Martin *et al.* 2008; Pasini & Garassino, 2011). Traces (burrows) constitute the bulk of the fossil record of the Southern Hemisphere family, Parastacidae (Hasiotis, 2002; Bedatou *et al.* 2008; Martin *et al.* 2008). As a result, the evolutionary history of Parastacidae is poorly understood (Martin *et al.* 2008) and additional fossil evidence is vital to unravelling the distribution patterns of this group (Feldmann *et al.* 2011).

Like all decapod crustaceans, crayfish have a rigid, calcified, cuticular exoskeleton covering the softer internal body parts (Luquet, 2012; Nagasawa, 2012). Despite offering protection from predators, the exoskeleton constrains growth of the organism. As such, the decapod exoskeleton is periodically moulted during ecdysis, after which the body size increases and a new exoskeleton is sclerotized (Greenaway, 1985; Brandt, 2002; Luquet, 2012). Prior to ecdysis, select crustacean taxa resorb calcium-carbonate and other cuticular minerals from the old exoskeleton (Luquet, 2012). In lobsters and crayfish, calcium storage involves the deposition of paired hemispherical structures in the cardiac stomach between the single-layered epithelium and a cuticle lining (Greenaway, 1985; Brandt, 2002; Luquet, 2012; Habraken *et al.* 2015). Such structures have been referred to as gastroliths (Travis, 1960, 1963; McWhinnie, 1962) or more correctly, bio-gastroliths, which differentiates them from ingested sediment particles and pathological 'stomach stones' (Wings, 2007). After moulting, the bio-gastroliths are passed to the gizzard, dissolved and resorbed to accelerate exoskeletal recovery and restart the ability to feed (Frizzell &
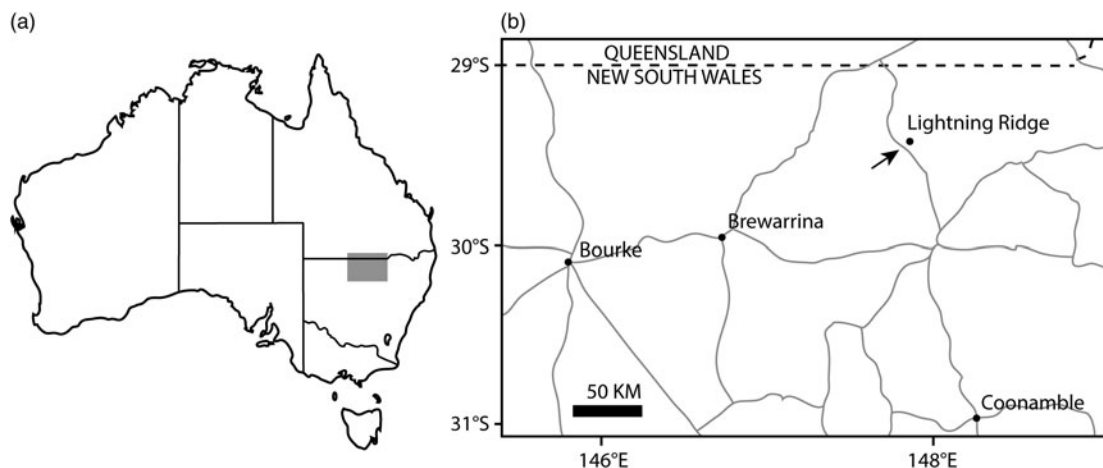
Fig. 1. Locality map of (a) Australia and (b) the Lightning Ridge region. Grey area in (a) depicts the expanded area in (b). Fossilized parastacid crayfish bio-gastroliths described here come from the Cenomanian-aged Griman Creek Formation in the vicinity of Lightning Ridge (arrow).

Exline, 1958; Travis, 1960; Glazer *et al.* 2013). Bio-gastroliths therefore act as temporary calcium-carbonate storage units (Ueno, 1980; Nagasawa, 2012).

Although widespread in extant decapods, fossil bio-gastroliths are exceedingly rare. The only records come from the Upper Jurassic Yixian Formation in China (Taylor *et al.* 1999) and the middle Eocene Clairborne Group in Texas (Frizzell & Exline, 1958). Similar calcium storage structures (dermoliths) have also been reported in Late Cretaceous isopods from Lebanon (Feldmann, 2009; Feldmann & Charbonnier, 2011). Here, we formally report on the first Cretaceous decapod bio-gastroliths, which come from the Cenomanian-aged Griman Creek Formation near the town of Lightning Ridge in central-northern New South Wales, Australia (Fig. 1). Although decapod bio-gastroliths from the Griman Creek Formation have been referred to on multiple occasions (Smith, 1999; Bell *et al.* 2019; Tucker & Tucker, 2019), they have not been formally described and their affinities have not been discussed. We describe these remains and discuss their implications for palaeobiogeography and as palaeoenvironmental indicators in the Griman Creek Formation.

2. Geological setting

Decapod remains described here derive from the Wallangulla Sandstone member of the Griman Creek Formation (Rolling Downs Group, Surat Basin). Near the town of Lightning Ridge (New South Wales), surface exposures of this interval are generally lacking; however, more than a century of small-scale opal mining, which is almost exclusively responsible for the extraction of fossils, permits observations of the geology underground. Subterranean exposures of the Wallangulla Sandstone member (Moore, 2002) exceed 25 m in thickness and include laterally extensive but discontinuous claystone lenses ('Finch Clay facies'; Scheibner & Basden, 1998) that are the sole source of commercial opal and opalized fossils, including those described here. These sediments are interpreted to have been deposited in freshwater lakes and lagoons on a lowland floodplain that drained into the epeiric Eromanga Sea, which lay to the north and northwest of the study area (Bell *et al.* 2019). Although chiefly freshwater (based on the diverse invertebrate fauna), rare marine vertebrates (aspidorhynchid teleosts, lamniform chondrichthyans, leptocleidid plesiosaurs) attest to distal connections between some of these water bodies and

the Eromanga Sea (Bell *et al.* 2019 and references therein). During Cenomanian time, Lightning Ridge would have been at a palaeolatitude of ∼60° S (Matthews *et al.* 2016) and probably had a mean annual temperature of ∼14 °C based on the diverse crocodylomorph fauna (Molnar, 1980; Molnar & Willis, 2001) and the minimum thermal tolerance of modern crocodylians (Markwick, 1998). The minimum depositional age of the Griman Creek Formation at Lightning Ridge has been radiometrically dated at 100.2–96.6 Ma (Cenomanian; Bell *et al.* 2019).

3. Systematic palaeontology

Arthropoda von Siebold, 1848
    Pancrustacea Zrzavý & Štys, 1997
    Malacostraca Latreille, 1802
    Eucarida Calman, 1904
    Decapoda Latreille, 1802
    Astacidea Latreille, 1802
    Parastacoidea Huxley, 1879
    Parastacidae Huxley, 1879
    Parastacidae gen. et sp. indet.

Material. LRF (Lightning Ridge Fossil, Australian Opal Centre, Lightning Ridge, New South Wales, Australia) 0022, 0058, 0171–0176, 0294–0305, 0381, 0419, 0433–0435, 0585–587, 0603–0665, 0720–0722, 0801, 1064, 1075–1084, 1168–1213, 1245–1285, 1326–1328, 1396, 1417, 1434, 1458, 1571, 1592, 1689–1693, 1752–1755, 1829–1831, 1844, 1871–1873, 1908, 1982, 2128–2129, 2177, 2201, 2210, 2775–2782, 2943, 3063, 3094, 3351–3357; AM F (Australian Museum, Sydney, New South Wales, Australia) 112635, 112669, 112966, 134336, 112969, 121705, 121706, 121708, 128045, 131602, 131603, 131606, 131608, 131609, 131684–131690, 131692–131700, 131701–131703, 131705, 131706, 131710, 131712–131714, 131717, 131718, 131724, 131726, 131727, 131735, 134528, 137347–137348; isolated bio-gastroliths.

Preservation. As with most fossils from the Griman Creek Formation at Lighting Ridge, the bio-gastroliths are pseudomorphs composed of precious and non-precious opal ($SiO_2.nH_2O$), which typically precludes replication of internal histology. However, concentric growth rings are often visible as surface features.
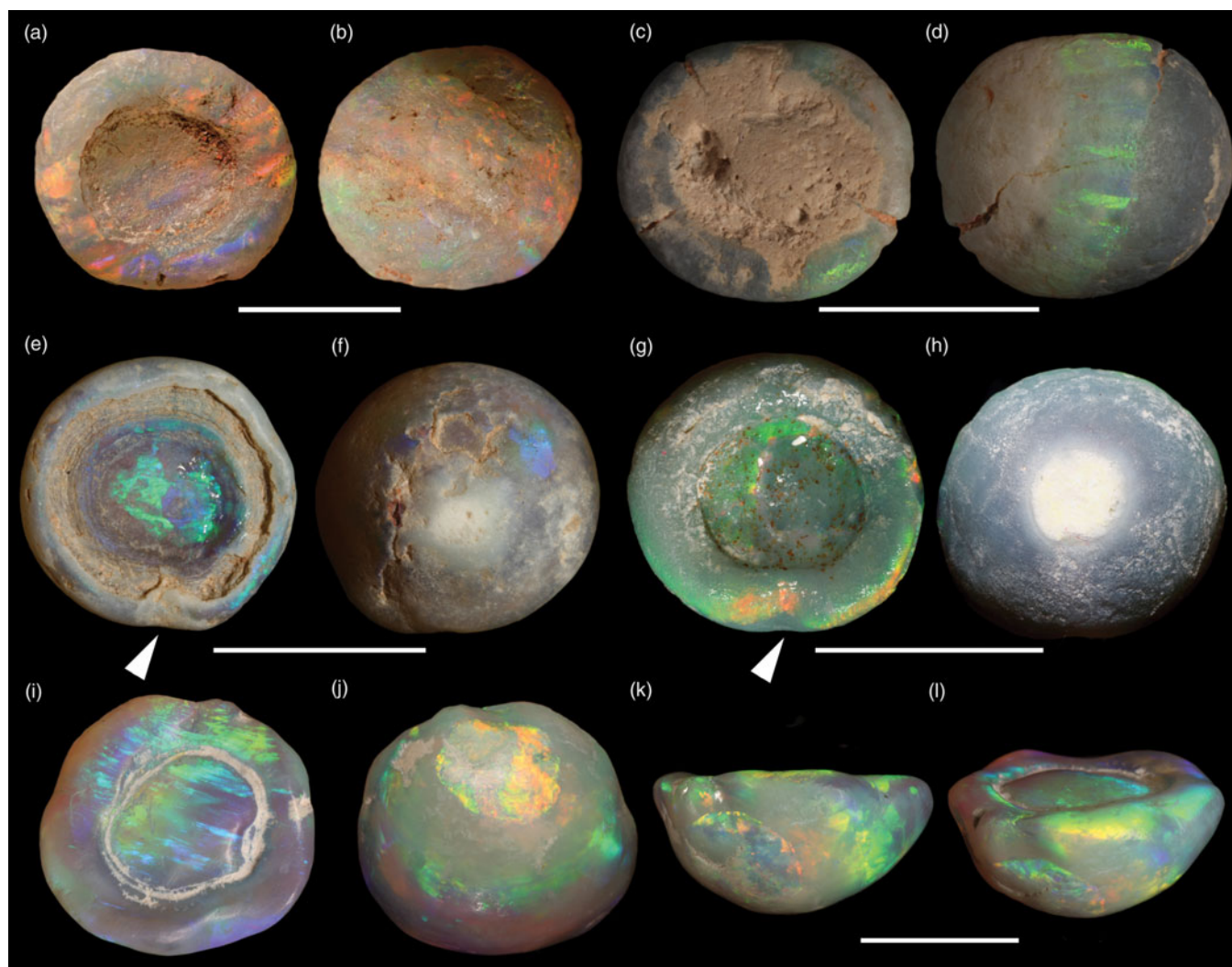
Fig. 2. (Colour online) (a, c, e, g, i) Internal and (b, d, f, h, j) external views of opalized parastacid bio-gastroliths from the Griman Creek Formation. (a, b) LRF3063; (c, d) LRF419; (e, f) LRF722; (g, h) LRF585; (i–l) LRF435; (k) lateral view; (l) lateral oblique view. Arrowheads demarcate the groove, or channel, on the outer rim. All scale bars = 5 mm. Photos: Robert A. Smith (Australian Opal Centre).

Description. Low-domed to nearly hemispherical bio-gastroliths with maximum diameters ranging from ~4 mm up to ~19 mm (e.g. LRF3355 and LRF3352, respectively) but most commonly 10–13 mm (Fig. 2; Table 1). They are slightly 'wider' than 'long'. In life, the long-axis would presumably have been oriented at roughly 45° (anterodorsally oriented in lateral view) to the long-axis of the animal as in modern crayfish (McWhinnie, 1962, fig. 1), while the domed (external) surface contacted the epidermis, and the concave (internal) surface contacted the stomach lining (Travis, 1960). In some specimens, the dome is comparatively low, and although predominantly smooth, many examples show random networks of shallow splits or cracks (e.g. LRF3352), and in others the texture is weakly knobbled (e.g. LRF3353). Presumably, these variations are due to incomplete development, partial resorption and/or postmortem decay.

Internally, the outer rim is thickened relative to the central portion of the disc. This outer rim displays concentric growth rings in well-preserved specimens (e.g. LRF722; Fig. 2e), whereas they are absent in others (e.g. LRF585, LRF1246; Fig. 2g). Growth rings appear to be accentuated where the rim has been broken or abraded, presumably soon after death. This outer rim is interrupted on one of the long edges by a shallow U-shaped groove or channel, which widens slightly towards the periphery of the element (Fig. 2e, g). The central depression (attachment scar) on the internal side may be concave (e.g. LRF722) or flat (e.g. LRF603, LRF1285) with a slightly roughened or irregular surface.

4. Discussion

Decapod bio-gastroliths are restricted to the Astacidea, a group that includes marine lobsters (Nephropoidea Dana, 1852) and freshwater crayfish. The latter group is divided into the Northern Hemisphere clade, Astacoidea Latreille, 1802 (consisting of Astacidae plus Cambaridae), and its Southern Hemisphere counterpart, Parastacoidea Huxley, 1879 (Parastacidae). This Northern–Southern Hemisphere dichotomy has its origins in the Jurassic Period, coinciding with the separation between Laurasia and Gondwana ~200–185 Ma (Ahyong & O'Meally, 2004; Martin *et al.* 2008; Crandall *et al.* 2009), although more recent phylogenetic hypotheses place this divergence in late Permian time ~261–268 Ma (Bracken-Grissom *et al.* 2014). The oldest parastacoid occurrence in Gondwana is established on the

Table 1. Table of measurements (in millimetres) for select crayfish bio-gastroliths from the Griman Creek Formation

Specimen no.	Max. length	Max. width	Height	
LRF 1186	7.26	7.21	3.79	
LRF 1200	7.56	7.07	3.30	
LRF 1592	8.63	8.20	3.56	
LRF 172	7.48	6.98	3.92	
LRF 435	17.59	16.65	9.12	
LRF 585	13.14	12.56	7.22	
LRF 722 (part)	15.09	14.30	6.81	
LRF 722 (part)	10.77	10.12	4.30	
LRF 722 (part)	7.87	6.98	3.36	
LRF 722 (part)	10.94	10.02	5.29	
	11.39	10.80	5.38	average

basis of burrows from the Upper Jurassic of Argentina (Bedatou *et al.* 2008), and burrows and body fossils firmly place this group in southern Australia by the Aptian (Martin *et al.* 2008). Morphologically, the Griman Creek Formation specimens resemble the bio-gastroliths of extant freshwater crayfish such as *Procambarus* Ortmann, 1905 and *Cherax* Erichson, 1846 (including *C. destructor* Clark, 1936, which is the species still found today around Lightning Ridge), sharing with them a smooth convex external surface and an internal surface dominated by a centrally depressed attachment scar, which is circumscribed by a thickened 'rim'. In fact, those of *C. destructor* are virtually identical in all respects (including size and morphology) to those of the Griman Creek Formation specimens (Fig. 3). Thus, an argument for the referral of the latter to *C. destructor* could be made. Combined molecular and morphological phylogenies of extant lobsters constrained by fossil occurrences suggest the genus *Cherax* may have persisted since 77 Ma (Bracken-Grissom *et al.* 2014). Other long-lived extant parastacoid taxa have estimated ranges close to 100 million years (e.g. *Engaeus* Erichson, 1846; Bracken-Grissom *et al.* 2014). Therefore, there is arguably a precedent for referral of the Griman Creek Formation specimens to the genus *Cherax*. As noted above, however, bio-gastrolith morphology is virtually identical between many modern genera (e.g. Frizzell & Exline, 1958), rendering any assignment of the fossil material to any of these taxa dubious.

While morphologically congruent with modern crayfish, the Griman Creek specimens are unlike the bio-gastroliths of extant marine lobsters (Nephropoidea), which tend to form loose aggregates of hundreds of small spicules that disaggregate rapidly postmortem (Herrick, 1911; Frizzell & Exline, 1958). Other bio-gastroliths occur in gecarcinid land crabs; however, these number four or more and are irregularly shaped (Greenaway, 1985; Luquet, 2012).

The assignment of these fossils to freshwater crayfish is further supported by the depositional environment of the fossiliferous horizons of the Griman Creek Formation at Lightning Ridge, which have been interpreted as representative of freshwater lakes (Bell *et al.* 2019). Importantly, at 96–100 Ma, deposition of the Griman Creek Formation at Lightning Ridge is concurrent with the late Albian – early Cenomanian regression of the epicontinental Eromanga Sea (Exon & Senior, 1976). Although some

waterways may have maintained distal connections to the Eromanga Sea (Bell *et al.* 2019), taxa that are regarded as exclusively marine (represented solely by aspidorhynchid fishes and sharks) are extremely rare in these deposits, whereas the diverse molluscan fauna (Newton, 1915; McMichael, 1956; Hocknull, 1997, 2000; Hamilton-Bruce *et al.* 2002, 2004; Kear & Godthelp, 2008; Hamilton-Bruce & Kear, 2010) attests to strictly freshwater conditions. Thus, the marine taxa may have been infrequent visitors to freshwater ecosystems rather than palaeoenvironmental indicators of marine conditions at Lightning Ridge (Bell *et al.* 2019). While modern marine decapods may also venture upstream into freshwater habitats (e.g. Chow & Fujio, 1987), this appears to be related to temporary occupation or hatching of planktonic larvae. In contrast, the ubiquity and relatively common occurrence of decapod bio-gastroliths in the Griman Creek Formation favours the assignment to a resident freshwater population. Indeed, bio-gastroliths are among the most commonly recovered fossils of any invertebrate or vertebrate from the Griman Creek Formation (P. R. Bell and E. T. Smith, pers. obs.), occurring throughout the opal fields over an area of several hundred square kilometres. Based on the above palaeoenvironmental, morphological and palaeobiogeographic arguments, we therefore assign the Griman Creek Formation bio-gastroliths to freshwater parastacid crayfish.

Fossil bio-gastroliths are extremely rare in the fossil record outside of the Griman Creek Formation, having only been identified in three taxa. Frizzell & Exline (1958) described bio-gastroliths from the middle Eocene Clairborne Group in Texas, which they named *Wechesia pontis* Frizzell & Exline, 1958 but did not assign them below Astacidea (their 'Nephropsidea'). These differ from the Griman Creek Formation specimens in their minute dimensions (typically ~0.2 mm in diameter), discoid (rather than hemispherical) shape, and the presence of radial grooves and a central depression on the external surface of the bio-gastrolith. The only other fossil crayfish bio-gastroliths belong to the cambarids (Astacoidea) *Palaeocambarus licenti* Taylor, Schram & Shen, 1999 and *Cricoidoscelosus aethus* Taylor, Schram & Shen, 1999 from the Upper Jurassic Yixian Formation in China (Taylor *et al.* 1999). Unlike both *Wechesia* and the Griman Creek Formation specimens, the Chinese bio-gastroliths were preserved as natural moulds (up to 7 mm in diameter) of the original structures within the foregut of articulated body fossils. Those authors briefly described them in two specimens of *Palaeocambarus*, one of which was described as having a 'rounded convex surface while the other possesses an outer depressed ridge with raised circular region' (Taylor *et al.* 1999, p. 124). These descriptions presumably refer to the impressions of the external and internal surfaces of the bio-gastroliths, respectively. Those of *Cricoidoscelosus* were mentioned but neither described nor figured. Nevertheless, we note that they superficially resemble the bio-gastroliths of the Griman Creek Formation and other crayfish in overall morphology (see above). Thus, fossil evidence for the mode of calcium storage in crayfish as a whole indicates a deep evolutionary origin that extends at least as far back as the Jurassic Period, although the shared presence of these bio-gastroliths in Astacoidea and Parastacoidea implies their presence at the time of divergence between these two groups, which has been dated to the middle Permian (Bracken-Grissom *et al.* 2014).

In Australia, parastacid body fossils from the Aptian–Albian Eumeralla Formation (Otway Group) in Victoria (Martin *et al.* 2008) and parastacid burrows from both the Eumeralla Formation and equivalent beds in the upper Strzelecki Group (= Wonthaggi Formation) establish their presence in eastern
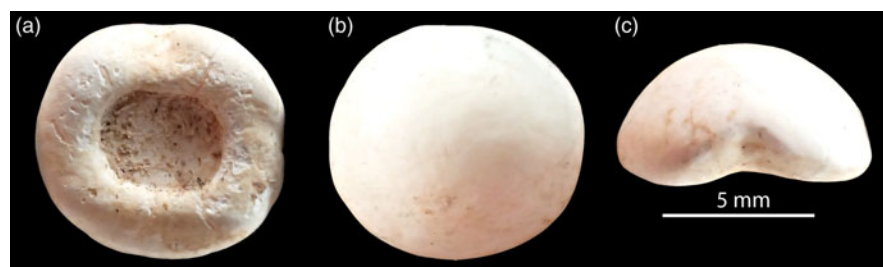
Fig. 3. (Colour online) Modern crayfish (*Cherax destructor*) bio-gastrolith collected from Lightning Ridge in the vicinity of the fossil representatives. (a) Internal; (b) external; and (c) posterior views.

Gondwana by middle Cretaceous time (Martin *et al.* 2008). Recent reports of crayfish bio-gastroliths from the Aptian–Albian marine deposits at Coober Pedy (South Australia) (Tucker & Tucker, 2019) are erroneous (E. Tucker, pers. comm. 2019), and in fact derive from the Griman Creek Formation. The remains from Victoria, estimated at 116 Ma (upper Strzelecki Group) and 106 Ma (Eumeralla Formation), also constitute the oldest parastacid body fossils from Gondwana (Martin *et al.* 2008). A variety of fossil invertebrate burrows occur throughout the Wallangulla Sandstone member (Griman Creek Formation) at Lightning Ridge; which of these, if any, represent crayfish burrows is a matter for further investigation. In other parts of the world, such traces are typically preserved in palaeosols (e.g. Bedatou *et al.* 2008, 2009; Genise *et al.* 2016; Nascimento *et al.* 2017), a facies not represented in the Griman Creek Formation (see Bell *et al.* 2019).

The recognition of bio-gastroliths from the Griman Creek Formation augments the scant fossil record of parastacids and has the potential to fill significant gaps in our knowledge of the evolution and palaeobiogeography of crayfish. However, the taphonomy of these structures is virtually unknown, especially in the Griman Creek Formation, where the unusual mode of preservation (i.e. as pseudomorphs in opal) may have contributed to their ubiquity as components of the fossil fauna; indeed, given the abundance of opalized molluscs in the Griman Creek Formation, there is an inference that opalization favoured $CaCO_3$ structures. But despite the abundance of bio-gastroliths, other crayfish body fossils are entirely lacking in the Griman Creek Formation. The implications are interesting. The unique suite of conditions postulated to have been responsible for opal formation in central Australia – involving regional acidic oxidative weathering following the regression of the inland sea – invoke a peak period of opal production (and, hence, fossil formation) from ~97 Ma to 60 Ma (Rey, 2013). Autochthonous microbes preserved within opal nodules at Lightning Ridge have even been used to suggest that opal formation was synchronous with the deposition of sediments (Watkins *et al.* 2011), a model that is consistent with evidence from vertebrate fossils that indicates of a combination of preservation modes, from specimens with defined internal features to full pseudomorphs lacking microstructure. Fossil bones preserving cancellous or spongiform histology indicate a cell-by-cell mineralization process that commenced prior to decomposition of the organic material. In the case of complete pseudomorphs, a slightly more protracted diagenetic history prior to opalization is likely (Pewkliang *et al.* 2004); however, the presence at deposition of opaline silica or silica in solution is inferred.

The size, abundance and wide distribution of crayfish within the Griman Creek Formation at Lightning Ridge implies they were a substantial food source for a range of predators. Bio-gastroliths are temporary calcium storage structures that develop several weeks prior to ecdysis, after which they are rapidly resorbed (Frizzell & Exline, 1958; McWhinnie, 1962). Frizzell & Exline

(1958, p. 273) commented that 'intervention of a predator, consuming the premolt animal, normally is required for deposition of the gastrolith in sediments', a role they asserted was normally played by fish and ducks in modern settings. Thus, crayfish bio-gastroliths exist in the gut for only a short period of time, representing a limited window during which they can be potentially incorporated into the sedimentary record. Based on the ratio of body length-gastrolith diameter in modern crayfish (11:1 to 13:1; Frizzell & Exline, 1958), the largest Griman Creek Formation individuals would have been up to ~250 mm in length. Birds and large predatory fish are both known from the Griman Creek Formation (Molnar, 1999; Bell *et al.* 2019) (although the known bird fossils represent individuals too small to have been viable crayfish predators), as are a variety of carnivorous theropod dinosaurs and marine reptiles (plesiosaurs) that might have fed on crayfish, either systematically or opportunistically.

The discovery of parastacid bio-gastroliths in the Griman Creek Formation indicates that this group was widely distributed across Australia by Cenomanian time and inhabited a variety of freshwater ecosystems, consistent with modern members of the clade. In Victoria, extensional tectonics associated with the Australian–Antarctic rift valley (represented by the Eumeralla Formation and upper Strzelecki Group) supported freshwater lakes and braided streams (Vickers-Rich *et al.* 1988; Constantine *et al.* 1998; Herne *et al.* 2018; Tosolini *et al.* 2018). The high palaeolatitute (~68° S; Matthews *et al.* 2016) and cold annual average temperatures (−6 to +5 °C) evoked for the Victorian localities imply a long history of cold-water adaptation in this group, a trait consistent with modern parastacids (Martin *et al.* 2008 and references therein). In the Griman Creek Formation, near-coastal freshwater lakes supported crayfish at a palaeolatitude of ~60° S (Matthews *et al.* 2016; Bell *et al.* 2019). Palaeotemperatures at Lightning Ridge may have been significantly warmer (~14 °C based on the diverse crocodylomorph fauna and the minimum thermal tolerance of modern crocodylians; Molnar, 1980; Markwick, 1998; Molnar & Willis, 2001). Crocodylomorphs, while present, are extremely rare in the Eumeralla Formation and upper Strzelecki Group (Poropat *et al.* 2018), and other cold-sensitive ectotherms such as turtles are neither as abundant nor as diverse in Victoria as they are at Lightning Ridge (Smith, 2010; Smith & Kear, 2013), where they are the most commonly recovered vertebrate remains (Bell *et al.* 2019).

5. Conclusions

The fossil record of Southern Hemisphere freshwater crayfish (Parastacoidea) is extremely sparse. The earliest fossil evidence of this group comes from the Upper Jurassic of Argentina and the uppermost Lower Cretaceous of Australia. Crayfish bio-gastroliths, identified here from the Griman Creek Formation in New

South Wales (eastern Australia), extend this record into the earliest part of the Upper Cretaceous (Cenomanian). The new specimens indicate that Australian parastacids were relatively widespread by middle Cretaceous time and had occupied a variety of freshwater ecosystems consistent with the modern ecology of this group. Bio-gastroliths in the Griman Creek Formation are some of the most commonly recovered faunal remains from this interval, which is in stark contrast to the global fossil record of these structures, and of parastacids more generally. The presence of fossilized bio-gastroliths in both parastacoid and astacoid crayfish indicates a deep origin for these structures – perhaps extending as far back as the Permian Period, based on divergence timing estimates for these groups – and that these calcium storage modes have remained virtually unchanged to the modern day. The recognition of such structures in the fossil record has the potential to unlock aspects of the cryptic evolutionary history of Parastacoidea; however, the morphological similarity between bio-gastroliths of various crayfish potentially limits their application to high taxonomic levels.

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